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# THE THORACIC MECHANISM OF A GRASSHOPPER, AND ITS ANTECEDENTS

BY  
R. E. SNODGRASS  
Bureau of Entomology,  
U. S. Department of Agriculture



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By R. E. SNODGRASS  
BUREAU OF ENTOMOLOGY  
U. S. Department of Agriculture

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## INTRODUCTION

The principal elements in the motor mechanisms of arthropods are the muscles and the body wall, though the blood often plays an important secondary part as a hydraulic medium. All movements, however, come primarily from muscle contractions. A contracted muscle, when it relaxes, must be actively extended before it can operate again, and therefore muscles generally occur in antagonistic sets. But the muscles of insects are not necessarily opposed by other muscles; the counter force may be produced by the elasticity of the part of the body wall on which a muscle is attached. For this reason it is often

found in studying the anatomy of insects that a muscle has no antagonist. Moreover, while most insect muscles are *muscles of motion*, some are *tensors* inasmuch as they appear merely to maintain rigidity between parts that are subject to strain from other muscles.

The ectodermal cell layer of the body wall, or epidermis (commonly known as the "hypodermis"), is covered externally by a cuticula of which the general constituent is probably chitin, but in which other substances are deposited to form hardened areas called *sclerites*. The nature of the sclerotizing substances in insects is not yet known, but it appears to be definitely established that the sclerotic areas of the cuticula are not places where the chitin is thicker or denser (Campbell, 1929). Sclerites are secondary formations in the body wall, and it would be both interesting and important to know the physiological processes that produce them, for we should then be better able to evaluate sclerites as morphological units.

The major plates of the body-wall of an insect are very definite structures that are consistently reproduced by the deposit of sclerotizing substances throughout the whole series of insect forms, and some of them appear to be homologous with corresponding plates in other arthropod groups. On the other hand, all parts of the insect skeleton called "sclerites" in descriptive entomology are not of equal value. Many of them are simply areas of larger plates which have become secondarily demarked by lines of inflection in the cuticula that have formed internal strengthening ridges. The so-called sclerites in such cases are in themselves of no significance. The important morphological features are the endoskeletal structures; these are the rafters, the joists, and the upright supports that give strength to the edifice and enable it to withstand the strain of the muscles pulling on its walls.

It frequently happens, however, that a primary region of sclerotization becomes broken up by a discontinuity in the hardening substance of the cuticula, thus producing true secondary sclerites. The intervening "membrane" may take the form of a narrow line of flexibility ("suture"), or it may cover a large part of the original hard surface and reduce the primary sclerotization to two or more widely separated plates. Or again, an original sclerotic area may be contracted to a relatively small sclerite, or it may be obliterated. It then becomes a question, if the primary plate has been given a name, whether we are to apply this name to the area originally occupied by the plate, or restrict it to the sclerotic remnants or remnant. It is the usual practice to apply the name only to the sclerite, whatever its extent, and, if the sclerite is obliterated, to say that the part in question is obsolete



or lost. This usage has convenience for descriptive purposes, but it is likely to confuse our morphological conceptions, since an anatomical part is the same thing regardless of the nature of its surface covering.

# I. GENERAL DISCUSSION

If all that has been written about the thorax of insects were true, or could be made to fit with our present knowledge of insect struc-

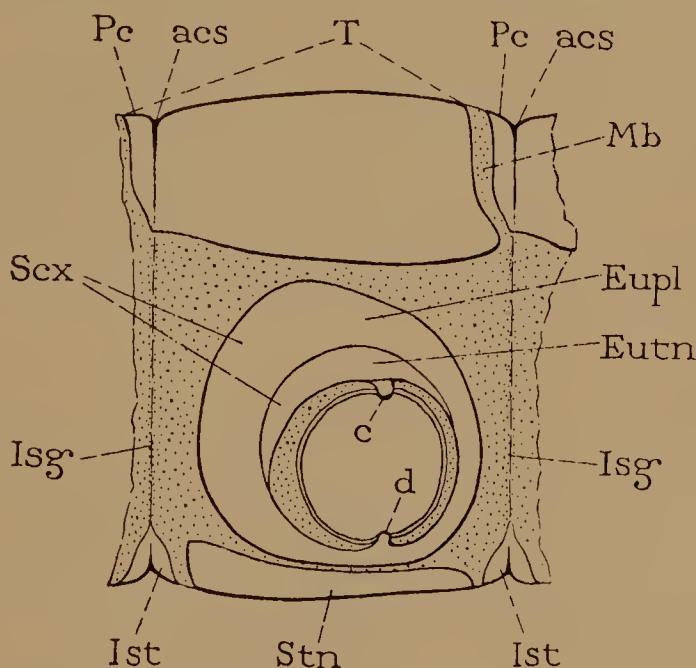


FIG. 1.—Diagram of the theoretical structure of a primitive thoracic segment.

The tergum (*T*) includes the segmental and preceding intersegmental sclerotization of the dorsum; the ventral sclerotization consists of a primary segmental sternal plate (*Stn*) and intersegmental intersternites (*Ist*); the pleural area is occupied by a basal subsegment of the leg, the subcoxa (*Scx*), divided dorsally into a eupleuron (*Eupl*) and a eutrochantin (*Eutn*).

*acs*, antecostal suture; *c*, *d*, dorsal and ventral subcoxo-coxal articulations; *Eupl*, eupleuron; *Eutn*, eutrochantin; *Isg*, primary intersegmental line; *Ist*, intersternite; *Mb*, secondary intersegmental membrane; *Pc*, precosta; *Scx*, subcoxa; *Stn*, primary sternite; *T*, tergum.

ture, there would be little need of prefacing a special description of the thoracic skeleton and musculature of the grasshopper with a general discussion. Science, however, is not a collection of facts but a concept in which to hold the facts. As our collections of facts become larger, our concepts must be altered and enlarged from time to time. Moreover, we often think that we have nicely fitted a fact into a mental container, only to discover presently that it does not fit at all, or that an important part of the fact has been left out. There is noth-

ing to do then but to discard the container or to remodel it as best we can to make it serve its intended purpose. The writer, therefore, finds it necessary to enlarge some general conceptions previously expressed concerning the nature of the thoracic mechanisms and their apparent evolutions from simpler origins, in order to accommodate new observations that must be admitted.

The primary intersegmental infoldings of the integument of arthropods are the original lines of attachment of the longitudinal muscles, and in most cases the principle longitudinal muscles are still attached on them. When the cuticula becomes sclerotized, the intersegmental inflections are usually converted into apodemal ridges, and a primary segmental plate is laid down in the dorsum and generally in the venter of each segment. In some cases the intersegmental sclerotizations take the form of narrow intersegmental sclerites alternating with the segmental plates. This condition is found more frequently in the ventral than in the dorsal region, though it exists dorsally in some insect larvae.

The typical sclerotization of the dorsum of any segment in an adult insect consists of a plate (fig. 1, *T*) which covers most of the dorsal area of the segment, and which is continuous anteriorly with the intersegmental sclerotization bearing the intersegmental fold or ridge (fig. 2 A, *Ac*). The definitive tergum, therefore, occupies a primary segmental region and the preceding intersegmental region; it bears anteriorly a submarginal, intersegmental ridge, or *antecosta* (fig. 2 A, *Ac*), marked externally by the *antecostal suture* (figs. 1, 2 A, *acs*), and it terminates anterior to this ridge and its suture in a narrow lip, or *precosta* (*Pc*).

The ventral sclerotization of the segment may take the same form as the dorsal sclerotization, as in the abdomen of most insects, where the definitive terga and sterna duplicate each other in structure (fig. 3). The functional intersegmental rings of the body in such cases are the posterior, non-sclerotized areas of the primary segments, and the definitive segmentation is clearly a *secondary* one. The sternal sclerotization, however, may preserve a more primitive condition, as in some of the chilopods (figs. 8, 15) and in the thorax of certain insects, where the primary sternal and intersternal plates remain independent (figs. 1, 2 A, *Stn*, *Ist*).

In the membranous areas of the lateral, or pleural, walls of the segment are implanted the bases of the segmental appendages. In most arthropods the basis of the appendage (coxopodite) is preserved as an integral limb segment. In the body segments of the chilopods, the thoracic segments of insects, and the ambulatory segments of decapod

crustaceans, however, it appears that the limb basis has become subdivided into a coxa and a subcoxa, and that the latter has been incorporated into the wall of the body segment (fig. 1, *Scx*), where it either forms a "pleuron" supporting the free part of the limb, or also the base of the wing, or it becomes degenerate and reduced to small sclerites having little significance or function.

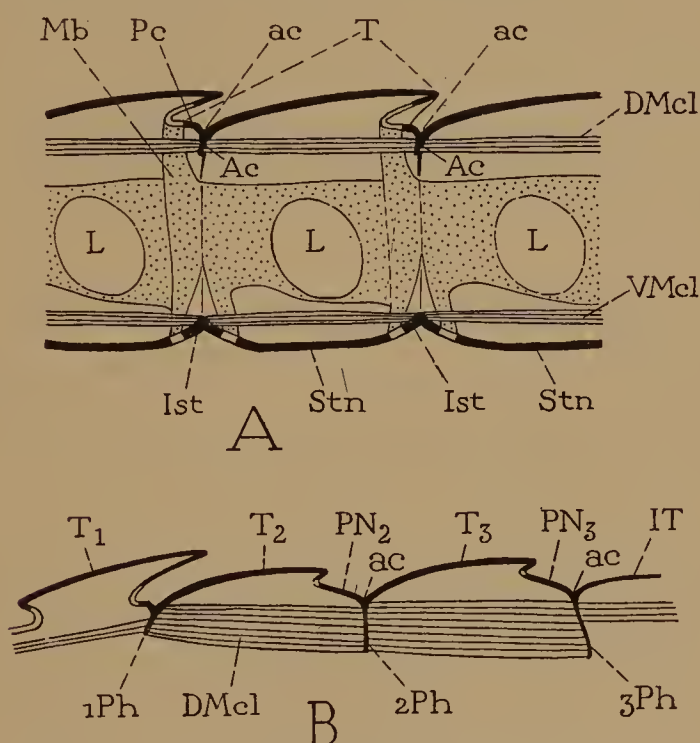


FIG. 2.—Diagram showing the relation of the longitudinal muscles to the tergal and sternal sclerites of the body.

A, three successive segments in which the terga include the primary intersegmental regions bearing the intersegmental ridges (*Ac*, *Ac*), but in which the primary sternites (*Stn*) and intersternites (*Ist*) are distinct. B, the tergal region of the thorax in an insect in which the precostae (A, *Pc*) are enlarged to form postnotal plates (*PN*).

*Ac*, antecosta; *ac*, antecostal suture; *DMcl*, dorsal longitudinal muscles; *Ist*, intersternites; *IT*, first abdominal tergum; *L*, positions of leg bases; *Mb*, secondary intersegmental membrane; *Pc*, precosta; *1Ph*, *2Ph*, *3Ph*, the three thoracic phragmata; *PN*, postnotal plates; *Stn*, primary sternite; *VMcl*, ventral longitudinal muscles.

#### THE THORACIC TERGA

The dorsal plates of the insect thorax never retain in all three segments the simple structure of the definitive abdominal terga, and in the Pterygota the mesothoracic and metathoracic terga are modified in various ways correlated with the development of the wings.

The prothoracic tergum (fig. 4, *T*<sub>1</sub>) always lacks an antecosta, and the principal longitudinal muscles (*DMcl*) that extend forward from

the anterior phragma of the mesotergum (*iPh*) run continuously through the prothorax and the neck (*Cv*) to be inserted on the post-occipital ridge of the head (*PoR*). This ridge, as the writer has elsewhere contended (1928), is evidently the intersegmental fold between the first and second maxillary segments. The neck, therefore, must be derived from the posterior part of the second maxillary, or labial, segment and from the anterior part of the prothorax, there being no satisfactory evidence of the existence of a separate neck segment. If so, the first postcephalic intersegmental line, or that between the labial and prothoracic segments (fig. 4, *iIsg*), must be contained in the membranized cervical region, where the protergal costa is lost. By the suppression of the primary intersegmental line between the head and

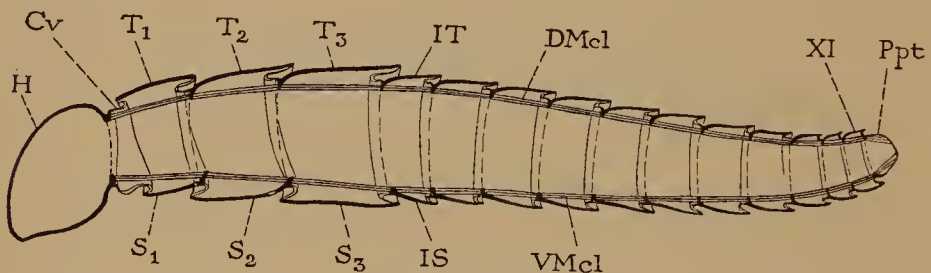


FIG. 3.—Diagram of the body segmentation of an insect, and the primitive relation of the longitudinal muscles to the definitive segmental plates of the body and to the head; showing the reversed overlapping of the sterna between the thoracic and abdominal regions.

*Cv*, cervix; *DMcl*, dorsal longitudinal muscles; *H*, head; *IS*, first abdominal sternum; *IT*, first abdominal tergum; *Ppt*, periproct, or terminal segment; *S1*, *S2*, *S3*, thoracic sterna; *T1*, *T2*, *T3*, thoracic terga; *VMcl*, ventral longitudinal muscles; *XI*, eleventh abdominal segment.

the thorax, giving continuity to the muscle fibers of two segments, the head acquires a much greater freedom of motion than it could have if it were attached to the body by an ordinary intersegmental membranous ring.

The loss of the protergal antecosta deprives the prothorax of the possibility of being a wing-moving segment, and there is nothing to suggest that the prothorax ever possessed movable organs of flight. The reduction of the primitive gnathal region of the body and its condensation into the head capsule, accompanying the transfer of the gnathal appendages to the head, shifted the center of gravity posteriorly in the insect's body, and the paranotal lobes of the second and third thoracic segments were developed into movable wings, leaving the prothorax as a free segment between the head and the pterothorax.

The most conspicuous modifications of the thoracic terga occur in the mesothorax and the metathorax of winged insects, where clearly



they are correlated with the part the terga of these segments play in the mechanism of flight. In the Apterygota the corresponding terga are simple plates showing none of the special characters of the wing-bearing plates of pterygote insects.

The first important tergal modifications connected with the development of the paranotal lobes into movable organs of flight pertain to the ridges upon which the dorsal muscles of the mesothorax and metathorax have their attachments. These ridges, which are the antecosta of the mesotergum, the antecosta of the metatergum, and the antecosta of the first abdominal tergum, bear each a pair of apodemal plates, varying in size, that project into the body cavity to give increased surfaces of attachment for the greatly enlarged dorsal muscles (fig. 2 B, *DMcl*) which have become depressors of the wings. The antecostal apodemes, primarily intersegmental, are the *thoracic phragmata* (*1Ph*, *2Ph*, *3Ph*).

The lengthwise pull of the dorsal muscles on the phragmata demands sclerotic continuity in the dorsum, since the function of these muscles as depressors of the wings depends on their ability to produce a dorsal curvature in the terga on the relaxation of the antagonistic tergo-sternal muscles. To insure action by the dorsal muscles the intersegmental membranes between the mesotergum and metatergum and between the latter and the first abdominal tergum must be practically eliminated, and their suppression has been accomplished either by a fusion of the succeeding terga, or by a forward extension of the precostal lips of the terga into the territory of the membranes. In the second case, the precostae become postnotal plates (fig. 2 B, *PN*<sub>2</sub>, *PN*<sub>3</sub>), often of large size, lying behind the true tergal plates of the mesothorax and metathorax (*T*<sub>2</sub>, *T*<sub>3</sub>), where they appear to be parts of these segments, to which, in fact, they do belong since they lie anterior to the antecostal sutures (*ac*, *ac*) which are the primary intersegmental lines.

In those insects in which the fore wings are the principal organs of flight, the second thoracic phragma becomes partially or wholly detached from the metatergum, and both the phragma and the postnotal plate establish a close association with the mesotergum, while the extremities of the postnotum commonly unite for security with the posterior dorsal angles of the mesothoracic epimera. In those insects in which the hind wings have taken on the chief function of flight, the middle phragma always remains attached to the metatergum, and the precosta is not enlarged. The third phragma may preserve its connection with the first abdominal tergum, as it does in the Orthoptera (fig. 25, *PN*<sub>3</sub>), but in most cases it becomes more or less separated

from the abdomen and, together with the precosta, becomes transferred to the metathorax, where the precosta forms a distinct post-notal plate united laterally with the epimera. Thus it is usually found that the segment which assumes the leading rôle in the flight mechanism is provided with a phragma at both its anterior and its posterior end.

Since the tergal plates of the mesothorax and metathorax are the intermediary elements in the wing mechanism between the dorsal mus-

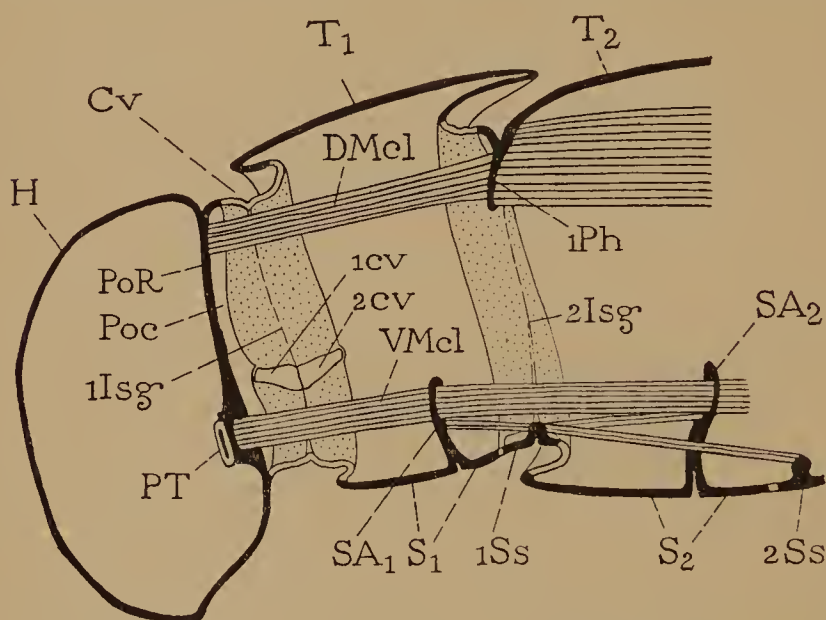


FIG. 4.—Diagram of the typical relation of the head and the prothorax in pterygote insects.

*Cv*, cervix; *1cv*, *2cv*, first and second lateral cervical sclerites; *DMcl*, dorsal longitudinal muscles; *H*, head; *1Isgr*, *2Isgr*, first and second primary intersegmental lines; *1Ph*, first thoracic phragma; *Poc*, postocciput; *PoR*, postoccipital ridge; *PT*, posterior arm of tentorium; *S1*, *S2*, thoracic sterna; *SA*, sternal apophyses; *Ss*, spinisternites; *T1*, *T2*, thoracic terga; *VMcl*, ventral longitudinal muscles.

cles of the segments and the bases of the wings themselves, it is clear that a proper execution of their function depends upon the ability of each to respond to the muscle tension at its ends with a dorsal curvature reaching its maximum at the transverse line between the wing bases. For this reason, as Weber (1924, 1925) has pointed out, the terga of the wing segments are provided with internal ridges so arranged that the force of the muscles will not merely deflect the anterior and posterior parts of the plates, but will be distributed gradually toward the middle from each extremity, and thus produce an even dorsal flexion with its apex between the fulcrum of the wings.

The posterior gradient of an alar tergum usually has the form of a *V-shaped ridge* with the apex directed forward and the arms diverging toward the posterior lateral angles of the tergum (fig. 5 B, *VR*). The anterior gradient is less commonly developed than the posterior one, but, when present, it generally consists of two ridges, the *parapsidal ridges* (fig. 5 B, *PaR*), converging from the anterior margin of the tergum toward the middle, where they usually terminate without meeting. In some insects the anterior part of the tergum is strengthened by a transverse *prescutal ridge* (*PR*). In addition to these more general endoskeletal structures of the tergum, there may be present also

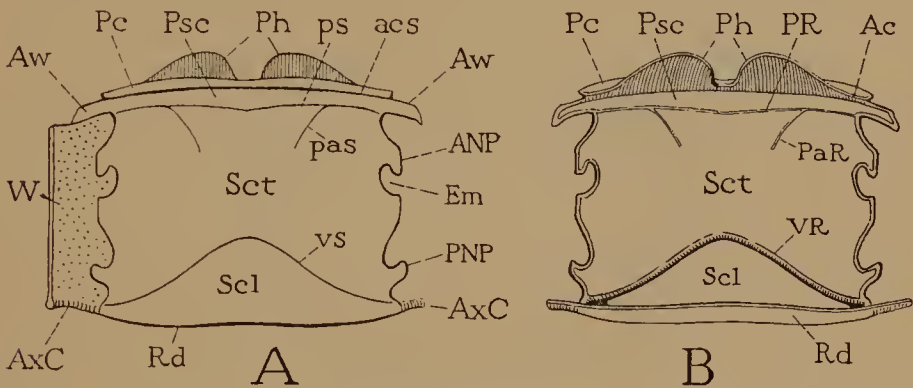


FIG. 5.—Structure of a wing-bearing tergum, not including a postnotum, diagrammatic.

A, dorsal. B, ventral. *Ac*, antecosta; *acs*, antecostal suture; *ANP*, anterior notal wing process; *AxC*, axillary cord; *Aw*, prealar process of tergum; *Em*, lateral emargination of tergum; *PaR*, parapsidal ridge; *pas*, parapsidal suture; *Pc*, precosta; *Ph*, phragma; *PNP*, posterior notal wing process; *PR*, prescutal ridge; *ps*, prescutal suture; *Psc*, prescutum; *Rd*, posterior fold, or reduplication, of tergum; *Scl*, scutellum; *Sct*, scutum; *VR*, V-shaped ridge; *vs*, suture of the V-ridge, or scuto-scutellar suture; *W*, base of wing.

a variety of accessory ridges, or even lines of flexibility in the tergal cuticula; but all such features are highly variable in different groups of insects, and homologies can be traced between them only within limited groups.

On the outer surface of the tergum the positions of the endoskeletal ridges are marked by the lines, or "sutures," of their inflection (fig. 5 A, *ps*, *pas*, *vs*). The tergal areas defined in this manner by the more constant of the inner structures can be identified as homologous in different insects, and some of them have been given distinctive names used in descriptive works (fig. 5 A, *Psc*, *Sct*, *Scl*). It is quite impossible, however, to follow the lesser modifications consistently through the various orders of winged insects, and attempts to do so have only led to confusion. In any case, it must be recognized that

the external "divisions" of the wing-bearing terga have no significance in themselves; they are merely incidental to the formation of the internal ridges by cuticular inflections, the ridges being the true functional structures adapting the tergum to its part in the flight mechanism.

#### THE THORACIC PLEURA

The lateral walls of arthropod segments, or the areas along the sides of the body between the terga and the sterna, when dorsal and ventral plates are present, may properly be designated the *pleural regions*. The pleural areas of the segments are primarily membranous, and

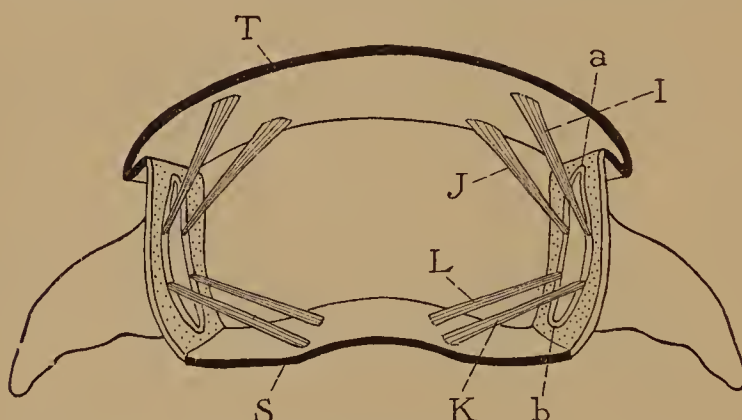


FIG. 6.—Diagram of the theoretical elementary musculature of the segmental appendages.

*a-b*, primitive dorsoventral axis of the appendage; *I*, tergal promotor muscle; *J*, tergal remotor; *K*, sternal promotor; *L*, sternal remotor; *T*, tergum; *S*, sternum.

within them are implanted the bases of the limbs (fig. 6). In some arthropods, as in many of the Arachnida, each limb basis occupies almost the entire space between the tergum and the sternum, and may be articulated to one or the other of these plates, or to both of them. In most cases, however, a membranous area partially or entirely surrounds the limb base. In this area there are sometimes developed true pleural sclerites, as in the chilopod family Geophilidae, where there is a series of lateral plates of the body wall lying between the terga and the leg bases (fig. 8 A, *pl*), or in the larvae of some insects where similar plates occur on the sides of the abdomen. In many arthropods, however, there are plates in the definitive lateral walls of certain segments that appear to have been derived from the bases of the appendages. While such sclerotizations are, therefore, not true pleural products, they are generally termed *pleurites*, and those of each side of each segment constitute collectively the so-called *pleuron* of the segment.



It is claimed by Becker (1923, 1924) that the pleurites, the coxae, and the trochanters in the Chilopoda are formed, during the development of the individual, from numerous schlerotizations in the lateral

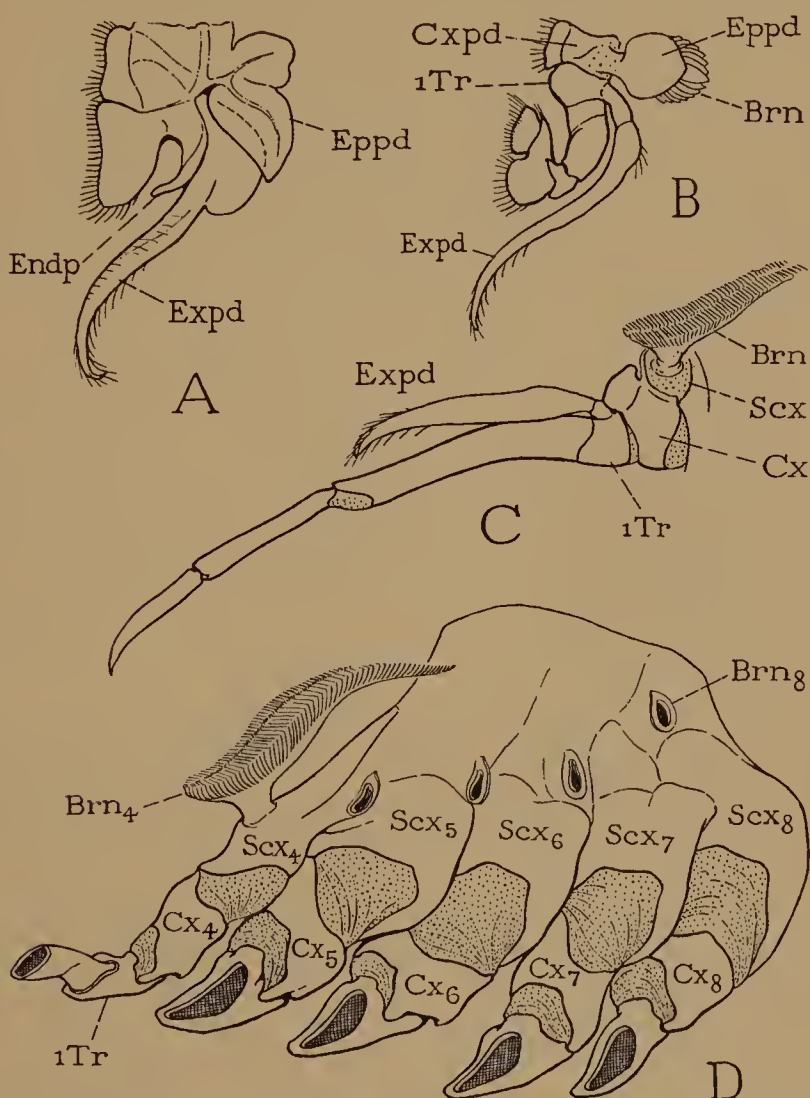


FIG. 7.—Maxillipeds and pleuron of a decapod crustacean, *Macrobrachium jamaicensis*.

A, first maxilliped, left, posterior surface. B, second maxilliped, right, anterior. C, third maxilliped, left, posterior. D, left pleuron, or inner wall of branchial chamber.

*Brn*, branchia, gill; *Cx*, coxa; *Cxpd*, coxopodite; *Endp*, endopodite; *Eppd*, epipodite; *Expd*, exopodite; *Scx*, subcoxa; *1Tr*, first trochanter.

walls of the body segments, which unite to form the definitive leg bases and the pleural sclerites of the adult. Though the apparent facts in the development of the chilopods may be as Becker describes them, it is difficult to see how they can be interpreted literally as repre-

senting the phylogenetic origin of the definitive pleural plates and the leg bases. It would seem more probable that they are ontogenetic phenomena only, and that Becker's observations really show simply that the pleurites and the bases of the legs have a common origin.

In the decapod crustaceans the inner walls of the gill chambers, which are covered externally by lateral folds of the carapace, are formed of large cuticular plates bearing the gills (fig. 7 D). Each plate, or pleuron, shows subdivisions ( $Scx_4$ - $Scx_8$ ) corresponding with the body segments of the ambulatory legs, and each subdivision bears a gill ( $Brn_4$ - $Brn_8$ ). In the second maxilliped (B) the homologue of the gill is borne on an epipodite (*Eppd*) which is distinctly carried by

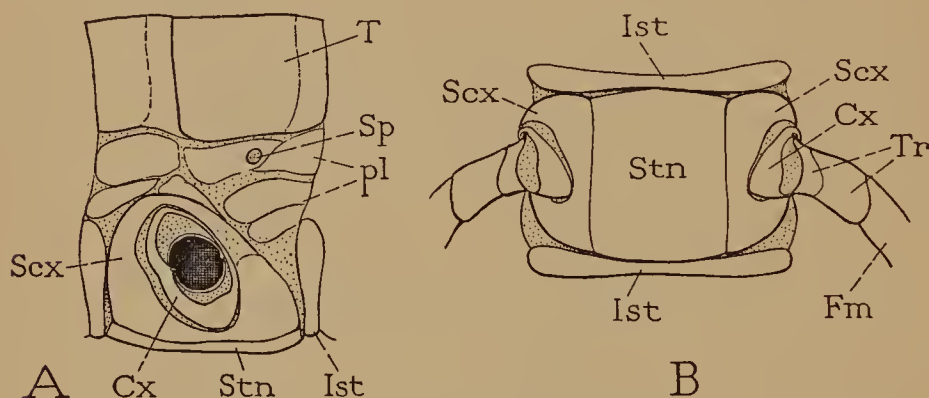
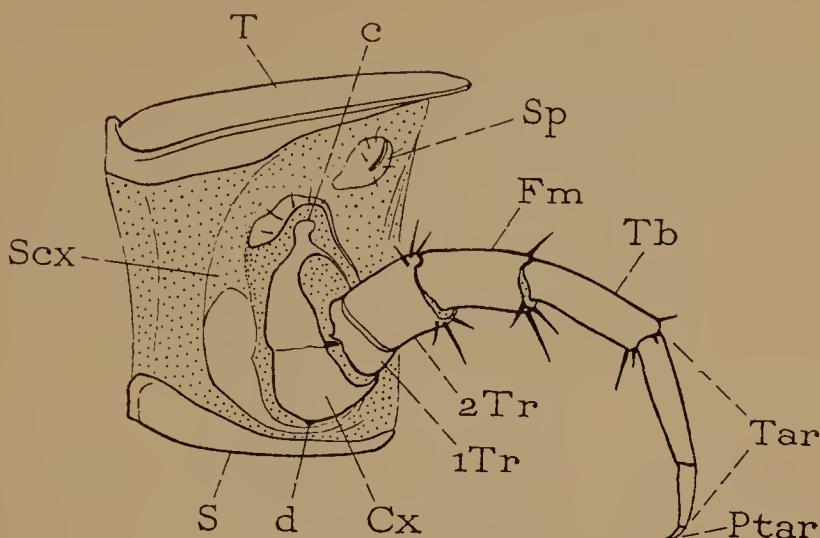


FIG. 8.—A body segment of *Strigamia bothriopus* (Chilopoda, Geophilidae).

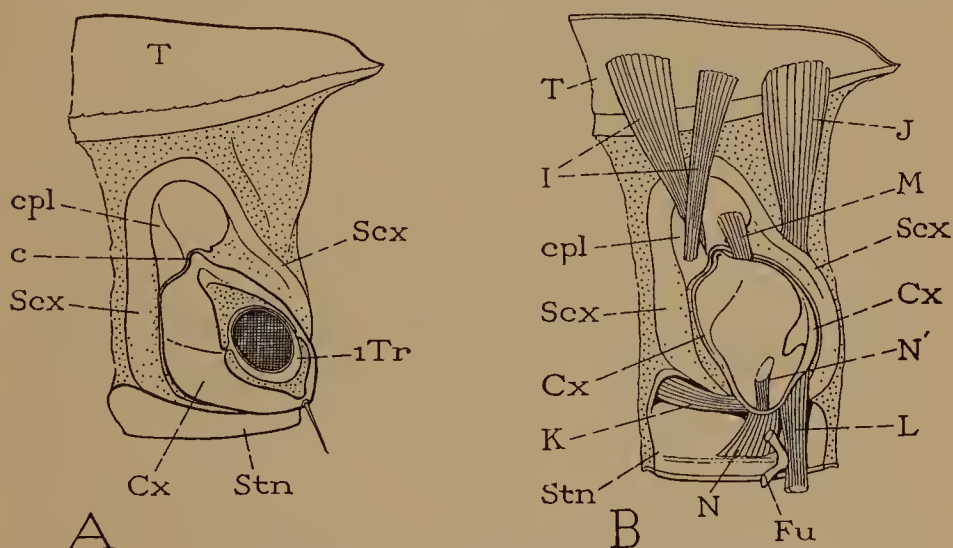
A, lateral view, with leg removed beyond the coxa. B, ventral view, including bases of legs. *Cx*, coxa; *Ist*, intersternite; *pl*, pleurites between the tergum and the subcoxa; *Scx*, subcoxa; *Sp*, spiracle; *Stn*, primary sternite; *T*, tergum; *Tr*, trochanter.

the basal segment of the appendage, or coxopodite (*Cxpd*). In the third maxilliped (C), however, the gill arises from a subcoxal part of the limb basis (*Scx*). In the ambulatory region (D) the gills on the pleuron are successively more and more removed from the coxae. It thus becomes evident that the pleural wall of the branchial chamber in the decapod crustaceans has been formed from dorsal extensions of the subcoxal parts of the leg bases, and that the coxae have acquired special articulations with the subcoxae. In the majority of crustaceans the leg base is an undivided coxopodite.

In the Chilopoda there is a definitely circumscribed subcoxal area about the base of each leg, which may be continuously sclerotized, as in *Strigamia* (fig. 8 A, *Scx*), or which may contain one or more sclerites, as in *Lithobius* (fig. 9), *Scolopendra*, or *Scutigera* (fig. 10). The coxa is usually articulated to a sclerotized part of the subcoxa dorsally (fig. 10 A, *c*), or ventrally (figs. 9, 15, *d*); but since the axis

FIG. 9.—A body segment and leg of *Lithobius* (Chilopoda), left side.

*c*, dorsal articular point of coxa; *Cx*, coxa; *d*, ventral articulation of coxa with subcoxa; *Fm*, femur; *Ptar*, pretarsus; *S*, sternum; *Scx*, subcoxa; *Sp*, spiracle; *T*, tergum; *Tar*, tarsus; *Tb*, tibia; *1Tr*, first trochanter; *2Tr*, second trochanter.

FIG. 10.—The leg base of *Scutigera forceps* (Chilopoda).

A, external view of base of a left leg and part of segment. B, internal view of base of right leg, showing muscles.

*c*, dorsal subcoxo-coxal articulation; *cpl*, supra-coxal plate of subcoxa; *Cx*, coxa; *Fu*, furca; *I*, tergal promotor muscles; *J*, tergal remotor muscle; *K*, sternal promotor; *L*, sternal remotor; *M*, subcoxo-coxal muscle; *N*, sternal adductor of coxa; *N'*, furcal adductor of coxa; *Scx*, subcoxa; *Stn*, segmental sternite; *T*, tergum; *1Tr*, first trochanter.

of movement in the coxa is always between its dorsal and ventral angles, we may presume that the chilopod coxa has had both a dorsal and a ventral articulation with the subcoxa (fig. 1, *c, d*), though one or the other, or both of the articulations (fig. 8) may lose the structure of definite articulating surfaces.

In the geophilid *Strigamia bothriopus* (fig. 8) the subcoxal area of the pleuron has the form of a complete basal limb segment (*A, Scx*), though its ventral margin is expanded and united with the sternum (*B*), and the coxa turns upon it by an obliquely vertical axis. In *Scolopendra*, *Lithobius* (fig. 9), and *Scutigera* (fig. 10) the subcoxal area is mostly membranous, but it contains one or more well-sclerotized plates.

The tergal muscles of the leg bases in the Chilopoda are inserted *not* on the coxae but *on the subcoxae*. In *Scutigera* the tergo-subcoxal muscles are strongly developed, those of each leg comprising a pair of anterior (promotor) muscles (fig. 10 *B, I*) inserted upon the dorsal plate (coxopleure, *cpl*) of the subcoxal region, and a single large posterior (remotor) muscle (*J*) inserted on the posterior dorsal margin of the subcoxal region.

The structure and musculature of the subcoxal region in the Chilopoda can leave little doubt that this area is the true base of the leg, which has become flattened into the lateral body wall, where, in most forms, its sclerotization has been more or less broken up and reduced. The sternal muscles of the leg base in the chilopods have gone over to the ventral rim of the coxa (fig. 10 *B*). They include an anterior (ventral promotor) muscle (*K*) and a posterior (ventral remotor) muscle (*L*). In *Scutigera* (fig. 10) the first of these muscles arises in the anterior lateral angle of the sternum, but in *Scolopendra* the corresponding muscle arises mesally on the anterior half of the sternum. The fibers of the posterior muscle in *Scutigera* (fig. 10 *B, L*) are mostly continuous from one coxa to the other, but a small anterior group on each side arises on the sternum at the base of the ligamentous endosternal furca (*Fu*). In *Scutigera* the coxa has no ventral articulation with the subcoxa or the sternum, but in those chilopods in which a ventral subcoxo-coxal articulation is present, the anterior and posterior ventral muscles (*K, L*) must act as promotors and remotors.

The base of the coxa in the Chilopoda is provided also with median dorsal and ventral muscle. The dorsal median muscle in *Scutigera* (fig. 10 *B, M*) consists of a flat band of short fibers arising on the dorsal plate of the subcoxa (*cpl*), and is inserted on the rim of the coxa just behind the dorsal articulation with the subcoxa. This muscle



appears to be a remotor of the coxa in *Scutigera*, though it may have an abductor function also. The ventral median muscles of *Scutigera* comprise two bundles of fibers, one arising medially on the sternum (fig. 10 B, *N*), the other (*N'*) arising on the lateral arm of the endosternal furca. These muscles are coxal adductors since the coxa has no fixed ventral articulation in *Scutigera*. The ventral coxal muscles are covered dorsally by large bands of trochanteral muscles that take their origin on the sternum. \*

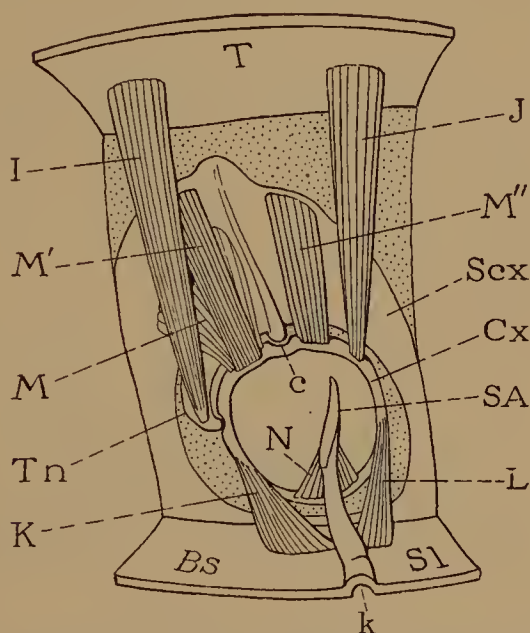


FIG. 11.—Diagram of the basal musculature of an insect leg.

*Bs*, basisternum; *Cx*, coxa; *I*, tergal promotor muscle; *J*, tergal remotor; *K*, sternal promotor (anterior rotator); *k*, furcal suture; *L*, sternal remotor (posterior rotator); *M*, abductor of the coxa; *M'*, *M''*, abductors of the coxa that become the basalar and subalar muscles in the wing-bearing segments of adult insects; *N*, adductor of the coxa; *SA*, sternal apophysis; *Scx*, subcoxa; *Sl*, sternellum; *T*, tergum; *Tn*, trochantin.

In the insects the sclerotic areas of the subcoxae of the legs evidently become the pleural plates of the thoracic segments. The tergal promotor muscle of the leg base (fig. 11, *I*) retains its connection with the subcoxa in the more generalized pterygote insects, being inserted on the trochantinal sclerite of the subcoxa (*Tn*) except when the trochantin is lost, the muscle then having its insertion on the anterior angle of the coxal base. The remotor muscle (*J*), which may be represented by several fiber bundles, is always inserted on the coxa or on coxal apodemes. The anterior and posterior sternal muscles (*K*, *L*) arise on the sterna or the sternal apophysis, or on the spinasternum.

The median coxal muscles are represented in insects by both dorsal (*M*) and ventral (*N*) fibers. In the wing-bearing segments of pterygote insects the first comprise three distinct groups of abductor fibers (*M*, *M'*, *M''*) arising dorsally on the pleuron, and inserted ventrally on the coxa both anterior and posterior to the dorsal articulation of the latter (*c*). The second and third muscles of this group (*M'*, *M''*)

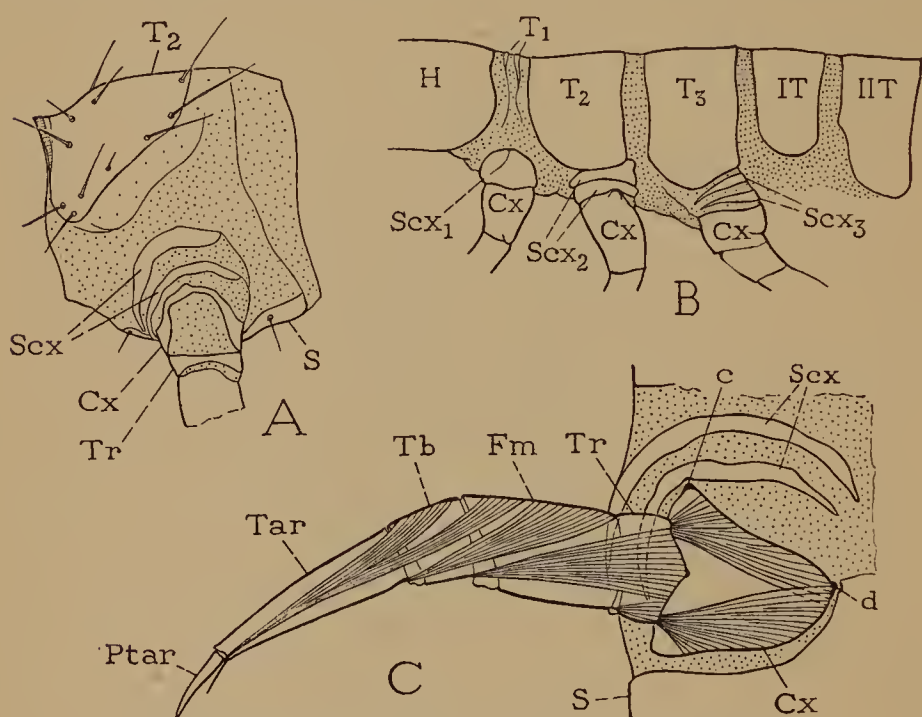


FIG. 12.—Thoracic pleural sclerites of Apterygota.

A, lateral view of left side of mesothorax of *Acerentomon doderoi* (from Berlese, 1910). B, thorax, base of head, and base of abdomen of *Isotoma* sp. (from Ewing, 1928). C, left mesothoracic leg turned forward, and lateral region of mesothorax of *Acerentulus barberi* (from Ewing, 1928).

*c*, dorsal articulation of coxa; *Cx*, coxa; *d*, ventral articulation of coxa; *Fm*, femur; *H*, head; *IT*, *IIT*, first and second abdominal terga; *Ptar*, pretarsus; *S*, sternum; *Scx*, subcoxa; *T<sub>1</sub>*, *T<sub>2</sub>*, *T<sub>3</sub>*, thoracic terga; *Tar*, tarsus; *Tb*, tibia; *Tr*, trochanter.

become wing muscles in the adult by the partial or complete detachment of the epipleural areas on which they arise to form the basalar and subalar plates of the wing base. The ventral median muscle of the coxa (*N*) is present in insects that lack a ventral coxal articulation; it arises on the sternal apophysis and functions as a coxal adductor.

In the Apterygota the subcoxa becomes rudimentary. In most of the Protura its sclerotization is reduced to two slender plates arched concentrically over the base of the coxa (fig. 12 A, C, *Scx*), as shown by Berlese (1910) and by Ewing (1928), though Prell (1913) has

described the pleural sclerotizations of *Eosentomon germanicum* as consisting of a number of small sclerites, which, however, fall into two concentric series. (See Snodgrass, 1927, fig. 8.) In the Collembola, as shown by Ewing (1928), the subcoxal sclerotizations of the mesothorax and metathorax (fig. 12 B,  $Scx_2$ ,  $Scx_3$ ) consist in each segment of two slender, supra-coxal arches; the subcoxal sclerotization of the prothorax ( $Scx_1$ ) is a single plate with an incomplete subdivision. In the Thysanura the subcoxal pleurites likewise take the form of two arches over the coxal base, or they become reduced to a single sclerite. The coxal and subcoxal musculature of the Apterygota has been but little studied.

In the thoracic segments of the Pterygota the subcoxae evidently become the sclerotized parts of the lateral segmental walls known as the *pleura* (cf. figs. 1 and 13). The ventral rim of each subcoxa, lying between the coxa and the sternum (fig. 13 A), may be reduced to a membranous fold, though in rare cases it contains a large plate (fig. 17,  $Ls_2$ ,  $Ls_3$ ), and in others a rudimentary sclerite (fig. 16 A,  $Ls$ ). In the majority of insects, as has been shown by Weber (1928, 1928 a), the ventral arc of the subcoxa has apparently fused with the primary sternite to form a laterosternite of the definitive sternum (figs. 13 B, 18 D,  $Ls$ ).

The coxa of insects is universally hinged to the subcoxa by a dorsal articulation (fig. 1, *c*); it may also have either an anterior articulation with the trochantinal piece of the subcoxa (fig. 13 B, *e*), or a ventral articulation (A, *d*) with the ventral rim of the subcoxa or with the subcoxal laterosternite. The trochantinal articulation of the coxa is peculiar to certain insects and is, therefore, probably a secondary one. The ventral articulation, however, so frequently recurs both in the Chilopoda (fig. 15, *d*) and in the more generalized insects (fig. 16 A, B, *d*) that there can be little doubt that the primitive axis of the subcoxo-coxal hinge was vertical or approximately so. The writer, therefore, would retract the opinion, expressed in a former study of the thorax (1927, pp. 34-36), that the primitive axis of the coxal movement was a horizontal one between anterior and posterior articulations with the eutrochantinal arch of the subcoxa. The ventral articulation of the coxa is highly variable in insects; it is always absent in the more generalized Pterygota that have a well-developed trochantin. In the members of the higher orders lacking a trochantin it is commonly present, but it is to be suspected in such cases that the articulation is a secondary one developed between the coxa and the sternum.

The usual trochantin of the pterygote pleuron (fig. 13 B, *Tn*) is clearly a remnant of a more extensive, primitive, supra-coxal sclerotization (fig. 1, *Eutn*) carrying the dorsal articulation of the coxa (*c*), which Crampton (1914) has named the *eutrochantin*, and which is best preserved in the ventral arch of the apterygote pleuron (fig. 12). The eutrochantin is retained as an independent sclerite also in the prothorax of the Plecoptera, but in all other Pterygota (fig. 13,

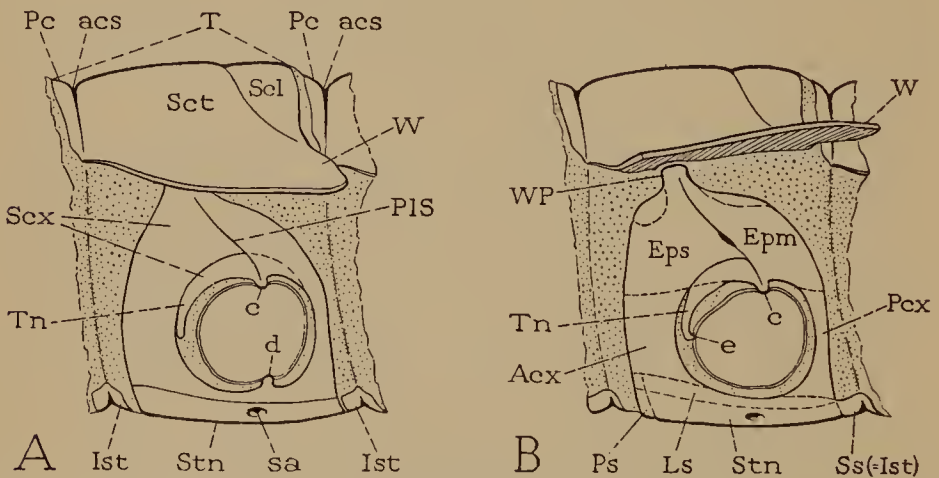


FIG. 13.—Diagrams suggesting the development of the pterygote pleuron from the subcoxa of the leg basis. (Compare with Fig. 1.)

A, subcoxal sclerotization (*Scx*) united ventrally with edge of primary sternite (*Stn*), its dorsal extremity prolonged upward as a wing support (B, *WP*), posterior part of entrochantin (fig. 1, *Eutn*) fused with eupleurial arch (fig. 1, *Eupl*) of subcoxa.

B, a fundamental structural condition of pleuro-sternal region of a wing-bearing segment: the area of subcoxa differentiated into an episternum (*Eps*), an epimeron (*Epm*), a precoxal bridge (*Acx*), a postcoxal bridge (*Pcx*), a laterosternite (*Ls*), and a trochantin (*Tn*); the definitive sternum includes the primary segmental sternite (*Stn*), the following intersegmental intersternite, or spinasternite (*Ss*), and a subcoxal laterosternite (*Ls*) on each side; the ventral coxal articulation (A, *d*) is lost, and coxa has a secondary anterior articulation with trochantin (*e*).

A, B) its dorsal and posterior parts unite or fuse with the upper arch of the pleuron (eupleuron), and only its anterior part remains as a free sclerite (fig. 13 B, *Tn*) carrying the anterior coxal articulation (*e*).

The elaborate pterygote pleuron has evidently been developed to give support to the paranotal lobes, or to the wings evolved from the latter. It is therefore strengthened by an internal ridge formed from a linear inflexion of its wall, the *pleural suture* (fig. 13 A, *PIS*), extending from the dorsal articulation of the coxa (*c*) upward to the wing support (B, *WP*). The area lying posterior to the pleural suture is the *epimeron* (B, *Epm*), that situated anterior to it and dorsal to



the trochantin is the *episternum* (*Eps*). The sclerotized parts of the subcoxa lying anterior and posterior to the coxa are the *precoxal* and *postcoxal bridges* (*Acx*, *Pcx*), or *precoxalia* and *postcoxalia*. The ventral wall, or infra-coxal arc, of the subcoxa, as already noted, probably unites in many cases with the edge of the primary sternum (*Stn*) to form a laterosternal element (*Ls*) in the definitive sternum, though it may be reduced to a separate sclerite or form a membranous fold between the coxa and the sternum.

All parts of the pleuron are subject to innumerable secondary modifications taking the form of sutures that subdivide the primary areas, or of membranous lines and spaces that break them up into separate sclerites. Such modifications are not necessarily homologous between different orders, but within an order or group of orders they may give valuable evidence of the evolution and interrelationships of the families and genera. An example of this is given by Shepard (1930) in a study of the secondary pleural sutures of Lepidoptera.

In the wing-bearing segments of the Pterygota two large pleuro-coxal muscles (fig. 11, *M'*, *M''*) become important muscles of the wings. These muscles evidently are derived from the abductor system of the coxa. In nymphal Orthoptera (fig. 27 C) the anterior muscle (*M'*) has its origin on the dorsal part of the episternum, the posterior muscle (*M''*) on the dorsal edge of the epimeron. In adult insects, however, the areas upon which these muscles are attached become partially or entirely separated from the pleuron and intimately associated with the base of the wing, the first lying before the pleural wing process, the second behind it. In this way the muscles come to function as wing muscles, though each retains its ventral attachment on the coxa.

The epipleurites ("paraptera"), or sclerites detached from the pleuron in connection with the coxo-alar muscles, include one or two episternal sclerites, or *basalares*, and usually a single epimeral sclerite, or *subalare*. The subalare is always completely detached from the epimeron in adult insects (fig. 14 A, B, *Sa*). A basalar plate, however, is not always present as a distinct sclerite; it frequently occurs as but an imperfectly separated lobe of the upper end of the episternum (fig. 14, *Ba*), and its area is sometimes marked only by the insertion of the anterior coxo-alar muscle (*M'*). Even when the basalare is distinct from the episternum, it is generally hinged to the upper edge of the latter in such a manner that it is deflected by the contraction of its muscle. Frequently there is present a second basalar muscle (figs. 27 C, E) having its origin on the pleuron or on the sternum.

The theory of the origin of the principal pleural sclerites of the Chilopoda and Hexapoda from subcoxal segments of the legs has much in its favor. There is little evidence, however, that a subcoxa is a primary segment in the general arthropod appendage. The limb bases of the Arachnida, Xiphosura, and most Crustacea are the primitive coxae (coxopodites), for there can be no doubt of the identity of the coxo-trochanteral articulation in all arthropods. The writer

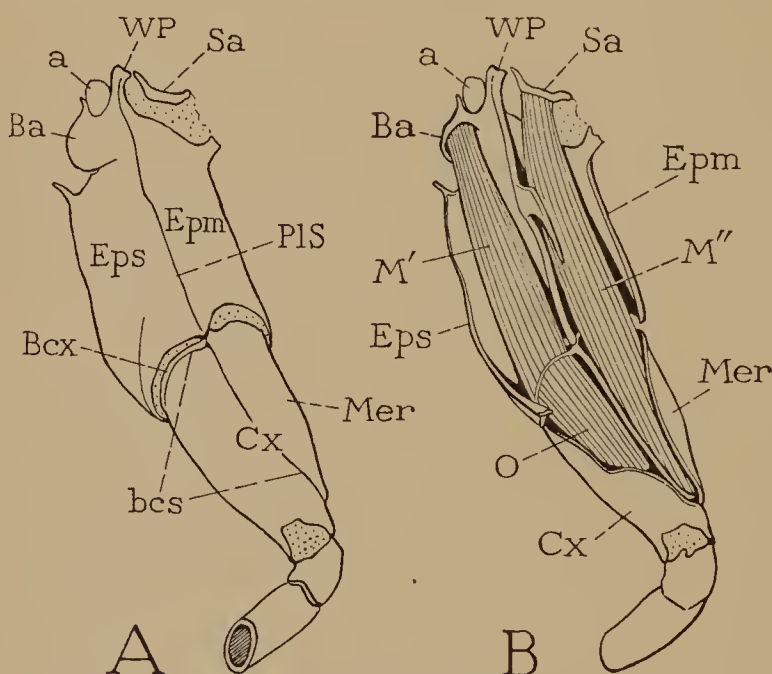


FIG. 14.—The mesopleuron and base of the middle leg of a scorpion fly, *Panorpa consuetudinis*.

A, external view. B, internal view, showing muscles. *a*, accessory sclerite of basalar lobe; *Ba*, basalar lobe of episternum; *bcs*, basicostal suture of coxa; *Bcx*, basicoxite; *Cx*, coxa; *Epm*, epimeron; *Eps*, episternum; *M'*, basalar muscle; *M''*, subalar muscle; *Mer*, meron; *O*, levator muscle of trochanter; *PLS*, pleural suture; *Sa*, subalar sclerite; *WP*, pleural wing process.

clearly was mistaken in suggesting in a former paper (1927, p. 33) that the large basal leg segments of the ticks (Ixodoidea) are subcoxal; and he now believes that the segmentation of the arachnid limb can be given an interpretation different from that proposed by Ewing (1928), who would make the basal segment in most cases a subcoxa. In the decapod crustaceans the inner walls of the gill chambers, as has already been pointed out, are evidently expansions of the subcoxal regions of the bases of the ambulatory legs, to which the coxae of the latter have become articulated; but there is no evidence of the presence of subcoxal segments in the limbs of the more generalized Crustacea. In the myriapods and insects, moreover, as the writer has else-

where shown (1928), there are no true subcoxal segments in the mouth part appendages. From the evidence at hand, therefore, it appears most in accord with the known facts to conclude that *the subcoxa, wherever it occurs as a basal leg segment, has been produced by a secondary subdivision in the primitive limb basis, or coxopodite.*

#### THE THORACIC STERNA

Sternal plates are by no means so constant a feature in the sclerotization of arthropod segments as are the tergal plates. They may be present or absent within the same major group, and, where present,

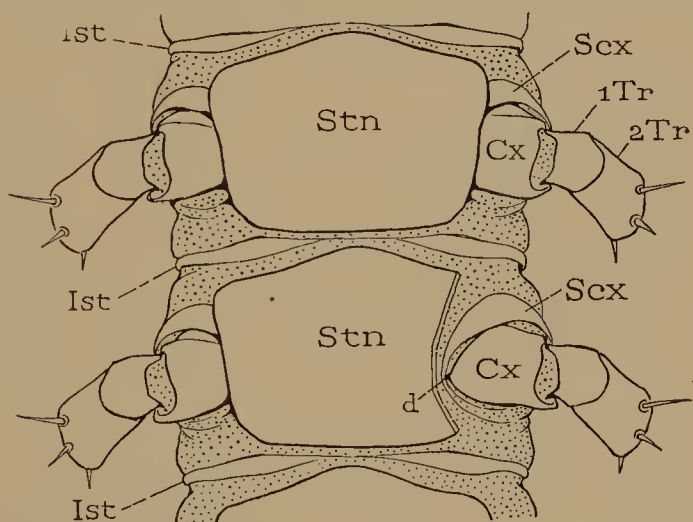


FIG. 15.—Sternites and leg bases of two consecutive segments of *Lithobius* (Chilopoda).

Cx, coxa; d, ventral subcoxo-coxal articulation; Ist, intersternite; Scx, subcoxa; Stn, segmental sternite; 1Tr, first trochanter; 2Tr, second trochanter.

they are often highly variable both in form and extent of development between closely related groups and in the different body regions of almost any species.

In adult insects the sternal mechanism of the thorax differs in three important respects from that of the abdomen, and the functional differences in the two body regions are reflected as three distinctive structural features in the sternal parts.

The first distinction to be noted in the sternal structure, as between the thorax and the abdomen, pertains to the segmental relations of the intersegmental sternites. In the abdomen of adult insects the intersegmental sclerotizations of both the dorsum and the venter are continuous with the segmental sclerotizations following, and the transverse inflexions in the cuticula of the primary intersegmental regions,

on which the fibers of the longitudinal muscles are attached, become the *antecostae* of the definitive terga and sterna (fig. 3). In the thorax, on the other hand, the ventral intersegmental sclerotizations either remain as small, free sclerites (fig. 1, *Ist*), or they unite with the posterior parts of the segmental plates preceding. The intersegmental sternites, or intersternites, of the thoracic region are the *spinasternites* (fig. 18 D, *Ss*), so-called because each usually bears a small median apodemal process, the *spina* (fig. 4). A spinasternite occurs typically between the prothorax and the mesothorax, and between the mesothorax and the metathorax; there is never a free spinasternite following the metasternum because the corresponding intersegmental element goes with the first abdominal sternum to form the antecosta of the latter, except where it is lost as a result of the degeneration of the first abdominal sternum. The first spinasternite is more commonly persistent than the second which is usually fused into the posterior part of the mesosternum, where it may become entirely obliterated.

The second structural difference between the thoracic and abdominal sterna accompanies the difference in the relations of the intersegmental sclerites to the segmental plates, but is not necessarily correlated with it. It consists of a reversal in the overlapping of the sterna. The successive abdominal sterna overlap regularly in a posterior direction, as do the terga of both the abdomen and the thorax (fig. 3). The sterna of the thorax, on the other hand, overlap *anteriorly*. The metathoracic sternum, therefore, stands as a dividing plate between the anteriorly overlapping sterna of the thorax and the posteriorly overlapping sterna of the abdomen (fig. 3, *S<sub>3</sub>*).

This reversal in the overlapping of the sternal plates as between the thorax and the abdomen is probably the oldest structural differentiation between the two regions of the body, for it is well shown in some of the Apterygota, particularly in *Japyx*, and is exhibited by all pterygote insects in which the thoracic sterna remain free from each other. It was probably, therefore, established when the thorax was first set apart as the locomotor center of the body, and has nothing to do with the development of the wings. Just what advantage accrues to the thoracic mechanism from the reversed relations of its sternal plates is not clear, but presumably it gives a better device for the movement of the legs or for the movement of the successive segmental plates on each other.

The third distinction between the thorax and the abdomen occurs in adult pterygote insects, and pertains to the attachments of the ventral muscles. We have assumed that the primitive attachments of the



fibers of the longitudinal muscles are on the intersegmental folds or on intersegmental sclerotizations (figs. 2, 3). The dorsal muscles throughout the length of the body, and the ventral muscles of the abdomen are thus attached, except where the anterior ends of the fibers may have migrated to the segmental regions of the definitive terga and sterna. In the thorax of adult pterygote insects, however, most of the sternal muscles are stretched between paired apodemal processes of the segmental sternites (fig. 4,  $SA_1$ ,  $SA_2$ ), except that the anteriormost fibers are inserted anteriorly on the head, while the posteriormost fibers extend into the abdomen. Only a few slender median muscles retain a connection with the intersternites ( $1Ss$ ,  $2Ss$ ). The paired

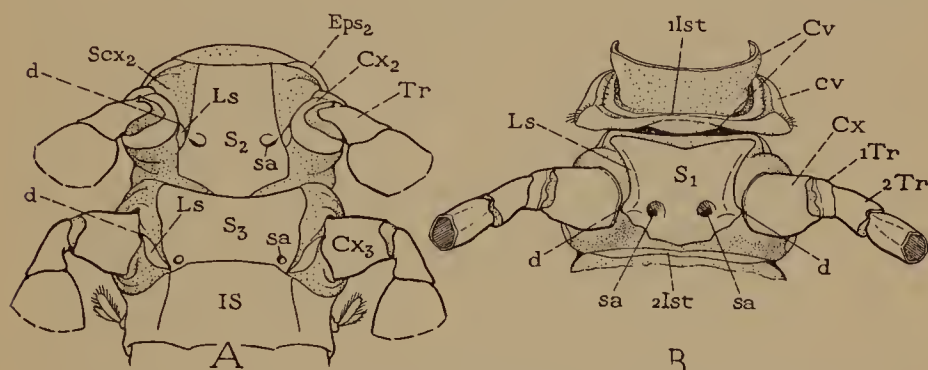


FIG. 16.—Sternal structure of ephemerid and odonate nymphs.

A, ventral surface of mesothorax, metathorax, and first abdominal segment of an ephemerid nymph, showing ventral articulations of coxae ( $d$ ) with subcoxal, laterosternal sclerites ( $Ls$ ).

B, ventral surface of neck and prothorax of an aeschnid nymph, showing direct articulation of coxae ( $d$ ) with laterosternal parts ( $Ls$ ) of the definitive sternum.

apophyses of the thoracic sterna are the so-called *furcal arms*, which in the higher orders are united upon a common median base and here constitute a true *furca*.

The anterior ends of the ventral muscle fibers, as we have noted, are attached on the back of the head. In orthopteroid insects the attachment is with the posterior arms of the tentorium (fig. 4,  $PT$ ), but this condition is clearly a secondary one since the posterior tentorial arms are tergal apodemes. In many adult insects, and in most holometabolous larvae, the anterior ventral muscles are inserted on the posterior part of the head wall. Morison (1927) enumerates three pairs of prothoracic sternal muscles in the honeybee, all of which are attached anteriorly on the lateral occipital regions of the head. In the caterpillars the corresponding muscles are inserted on apodemes of the ventral margin of the foramen magnum. In all such cases the insertion points of the ventral head muscles must have acquired their present positions

by a migration from the true sternal region of the last head segment, which is the membranous floor of the neck behind the base of the labium.

The ventral muscles of the thorax retain apparently the primitive condition in the larvae of most holometabolous insects. In the caterpillar, for example, the principal longitudinal ventral muscles consist of two wide bands of fibers lying to each side of the ventral nerve cord, extending through the entire length of the body, *and attached regularly on the intersegmental folds* as are the dorsal longitudinals. External to the dorsal and ventral intersegmental muscles of the caterpillar there is an intricate complex of small muscles disposed in all directions against the wall of each segment.

In certain larval forms, as in some Coleoptera, the attachment of the ventral body muscles shows a condition intermediate between the usual larval condition and that of the adult. In the larva of *Dytiscus*, for example, as shown by Speyer (1922), though most of the ventral thoracic muscles are intersegmental, being attached either to processes of the intersegmental folds or to transverse ligaments arising from the folds, some of the fibers extend between segmental furcal apophyses, which are present on each primary sternal region of the thorax. The ventral muscle bands of the thorax are continued into the abdomen, some of the fibers of the first abdominal segment being attached anteriorly on the intersegmental fold behind the metathorax, others on the furcal arms of the metasternum. In the adult of *Dytiscus* (Bauer, 1910) all the ventral muscles of the thorax are interfurcal in their attachments, and none extends from the thorax into the abdomen.

Ventral muscles from the thorax into the abdomen are absent in the adult stage of many pterygote insects (fig. 35), though they may be present in the larval or the nymphal stages. In the nymph of *Psylla mali*, according to Weber (1929), two bundles of fibers diverge from the base of the metafurca to the anterior edge of the second abdominal sternum, but these muscles, Weber says, are lost in the adult.

In some insects, however, the ventral thoracico-abdominal muscles are present in the adult stage. They are well developed in the cockroach (*Blatta orientalis*), comprising here three pairs, the first arising on the second spina, the second on a ligamentous bridge between the bases of the metasternal apophyses, the third on the apophyses, all of which are inserted posteriorly on the anterior margin of the second abdominal sternum. The fibers arising on the metapophyses form the anterior ends of the ventral longitudinal muscle bands of the abdomen. In *Gryllus*, Voss (1905) describes a median pair of muscles arising on the metafurca which branch posteriorly to the third, fourth, and

fifth abdominal sterna, and two lateral groups on each side which go to the parasternal plates of the second abdominal segment. In the Cicadidae ventral muscles extend from the metathorax to the second abdominal sternum. In the Tenthredinidae, according to Weber (1927), a pair of muscles extends from the metafurcal arms to the second sternum of the abdomen, and in the honeybee Morison (1927) describes two corresponding pairs of muscles going from the metafurca to the anterior margin of the second abdominal segment. Inasmuch as these muscles, which represent the ventral muscles of the first abdominal segment, have no connection with the first abdominal sternum, it is evident, as Morison points out, that their insertions, normally on the intersegmental anterior edge of the first abdominal sternum, have been secondarily transferred to the furcal apophyses of the metathoracic sternum. In the Ephemera, however, Dürken (1907) records the presence of a pair of muscles attached anteriorly on the bases of the metasternal apophyses and posteriorly on the anterior margin of the *first* abdominal sternum. These muscles would appear to correspond with the furco-spinal muscles, which are present in the prothorax of the grasshopper (fig. 35, 61).

Even a brief review of the comparative musculature of larval and adult holometabolous insects thus shows that there takes place during metamorphosis a rearrangement in the attachments of the ventral muscles of the thorax, and, in some cases, of those of the first abdominal segment, as a result of which most of the persisting fibers lose their intersegmental connections and acquire segmental attachments on the furcal apophyses of the thoracic sternal plates.

The larval condition of intersegmental muscle attachments is clearly a more primitive one than that of the adult. The adults of insects with incomplete metamorphosis resemble those of holometabolous forms in having the principal ventral muscles attached on the furcal arms. Therefore, we must suspect that the latter condition is one secondarily acquired in all pterygote insects, and that it has come about during the evolution of the thorax as a specialized locomotor region of the body. Since the transposition of the ventral muscles takes place in the prothorax as well as in the other two thoracic segments, we cannot attribute its inception to the development of the wings. As yet, however, we may draw only tentative conclusions concerning the evolution of the ventral musculature of the thorax, since our knowledge of the nymphal muscles in hemimetabolous insects and of both the larval and adult muscles in the more generalized holometabolous forms is very incomplete; but the facts known point strongly to the transformation suggested above.

An alteration in the attachment of the ventral muscles similar to that which evidently has taken place in insects may be observed also in the Chilopoda, here between members of different families. In the Geophilidae and in *Lithobius* the ventral longitudinal muscles consist principally of two flat, widely-separated bands of fibers lying close against the body wall and inserted on intersegmental sclerotizations.

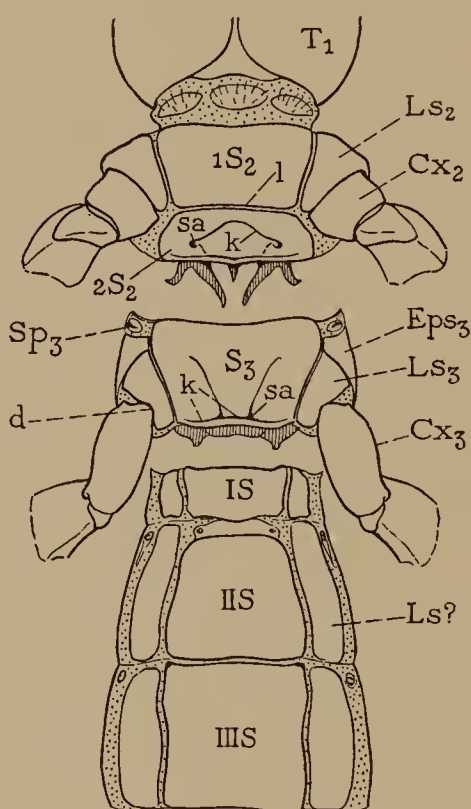


FIG. 17.—Ventral view of the base of the prothorax, the mesothorax, the metathorax, and the base of the abdomen of the large South American embiid, *Cylindrachaeta spegazzinii*.

*d*, ventral articulation of coxa with subcoxal laterosternite (*Ls*); *k*, furcal suture; *l*, secondary suture of mesosternum; *Ls*, laterosternite; *1S2*, anterior plate of mesosternum; *2S2*, posterior plate of mesosternum (furcasternite); *T1*, ventral fold of protergum.

In *Scolopendra* and *Scutigera*, on the other hand, both the longitudinal ventral muscles and many other muscles of each segment are attached on two ligamentous supports that arise from the posterior parts of the segmental sternites. In *Scolopendra* each ligament has a separate origin on the sternum; in *Scutigera* the two ligaments in each segment arise from a common base, forming thus a furca-like structure (fig. 10 B, *Fu*) suggesting that of the higher pterygote insects.

It is scarcely possible that there is any genetic relation between the furcal apophyses of insects and the muscle-supporting structures of



*Scolopendra* and *Scutigera*, but it is clear that the muscle attachments have been altered by a transposition which is of a parallel nature in the two cases.

In the Chilopoda the sternal plates are uniformly developed throughout the length of the body. In *Strigamia*, *Lithobius*, and *Scolopendra* there is a series of alternating segmental *sternites* (figs. 8 B, 15, *Stn*) and intersegmental *intersternites* (*Ist*). The intersternites are lacking in *Scutigera*; they are highly developed in the geophilid *Strigamia bothriopus*, where their lateral ends extend upward on the sides of the body between the subcoxae (fig. 8 A), but they are small and inconspicuous in *Lithobius* (fig. 15). In both the geophilid and lithobiid as we have seen, the longitudinal ventral muscle bands have their attachments on the intersternites.

The presence of alternating sternites and intersternites in the chilopods might suggest that this condition was the primitive one in insects, and that the intersternites (spinasternites) have remained free in the thoracic region or have united with the preceding sterna, while they have fused with the segmental sternites following in the abdomen. In the odonate larva shown at B of figure 16 there is a long intersegmental sclerite (*2Ist*) between the posternum (*S<sub>1</sub>*) and the mesosternum suggestive of the intersternites of the Chilopoda, and the fold (*1Ist*) in the ventral side of the neck (*Cv*), which bears the cervical sclerites laterally (*cv*), appears to be likewise an intersternite between the labial segment and the prothorax. In the Acrididae the spinasternite between the prothorax and mesothorax (fig. 21, *Ss*) is a well-formed plate attached to the prosternum (*S*); that between the mesothorax and metathorax is indistinguishably fused into the posterior border of the mesosternum, though the spina persists (fig. 31, *2Spn*). In many insects the first spinasternite is a free sclerite, and in the Blattidae both the first and the second are distinct plates (fig. 19 A, *1Ss*, *2Ss*).

The definitive thoracic sterna of most insects are undoubtedly composite structures. The first and second intersternites are usually contained in the posterior parts of the prosternum and mesosternum, respectively, or at least are closely associated with them, though the first frequently retains its independence. The ventral arcs of the subcoxae contribute laterosternal elements in many insects. The evident union of the ventral rim of the subcoxa with the sternum has been noted in the Hemiptera (Heymons, 1899, Snodgrass, 1927), but Weber (1928, 1928a) has given ample reasons for believing that this fusion of subcoxal elements with the primary sternum has taken place in the majority of insects. The frequent ventral articulation of the

coxae with the lateral margins of the sternum in generalized insects (figs. 12 C, 16 B, *d*) is further evidence that the sternum in such cases includes the infracoxal parts of the subcoxae, especially since it is found that, where distinct subcoxal laterosternal sclerites exist (figs. 16 A, 17, *Ls*), the coxae articulate with these sclerites (*d*).

It is difficult to find in the insects a good example of a simple primary sternal plate, comparable with the sterna of the Chilopoda (fig. 15), that does not contain either the following intersternite or subcoxal laterosternal elements, or both. In the mesothorax and metathorax of the ephemerid nymph shown in figure 16 A, the sterna ( $S_2$ ,  $S_3$ ) may contain the intersternites, but the two small sclerites in each segment (*Ls*, *Ls*) that articulate between the sternum and the coxa on each side appear to be the only remnants of subcoxal laterosternites. In the large embiid *Cylindrachaeta* (fig. 17) laterosternal plates ( $Ls_2$ ,  $Ls_3$ ) likewise are distinct, though the intersternites are clearly united with the primary sternites. In the prothorax of the aeschnid larva shown in figure 16 B the intersternite (*2Ist*) is independent of the sternum, but the laterosternites (*Ls*) are fused into the lateral sternal margins.

These several forms make it clear that the definitive thoracic sternum of insects is typically a compound plate. It consists of a *primary sternite* (fig. 18 A, B, *Stn*), to which may be added the succeeding *intersternite* (*Ist*), which becomes the *spinasternum* (C, D, *Ss*), and a pair of *laterosternites* (D, *Ls*, *Ls*) derived from the ventral arcs of the adjoining subcoxae (B, C, *Scx*).

The possession of paired apophyses, or *furcal arms*, is characteristic of the thoracic sterna of all pterygote insects. The apophyses arise from the sternal plates between the bases of the legs, and their outer ends are usually closely attached, either by fusion or by short muscle fibers, to the inner ends of the corresponding pleural apophyses.

Weber (1928, 1928a) advances the view that the sternal apophyses are primarily invaginations formed on the line of union between the primary sternites and the subcoxal laterosternites. In some insects, however, in which there are laterosternal plates not united with the sterna (figs. 16 A, 17), the origins of the sternal apophyses (*sa*) are still well within the sternal margins; and in an aeschnid nymph (fig. 16 B) the apodemal invaginations (*sa*, *sa*) are removed from the apparent margins of the laterosternite sections (*Ls*) of the definitive sternum. From evidence of this nature the writer would regard the sternal apophyses as invaginations in the primary sternal plate itself (fig. 18 B, *Stn*), though there is much in favor of Weber's view. The mesosternum of wingless females of the black aphid, *Aphis fabae*,

Weber (1928a) says, presents a case in which there can be no doubt that the furca arises at a point between the basisternite, the furcaster-nite, and the subcoxal laterosternite.

In the higher insects the sternal apophyses approach each other in each segment and unite upon a common basis produced by a median

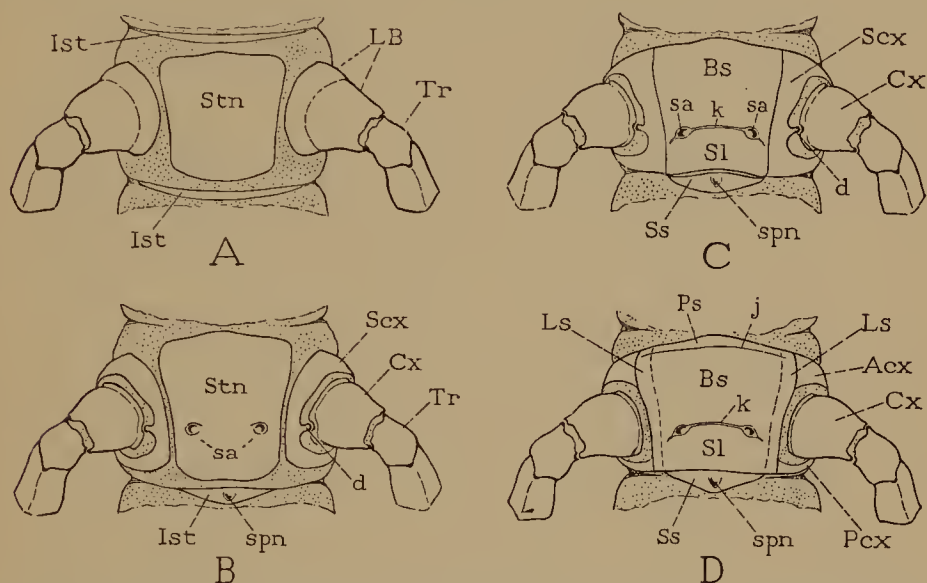


FIG. 18.—Diagrams suggesting the theoretical evolution of a thoracic sternum.

A, primitive condition in which the ventral sclerotization consists of alternating segmental sternites (*Stn*) and intersegmental intersternites (*Ist*); the leg basis (*LB*) is an undivided coxopodite.

B, primary sternite marked by the pits (*sa*) of a pair of internal apophyses, intersternite (*Ist*) by the pit (*spn*) of a median process, or spina; leg basis (*A, LB*) subsegmented into subcoxa (*Scx*) and coxa (*Cx*), articulated dorsally and ventrally (*d*).

C, area of primary sternite (*A, B, Stn*) divided into basisternum (*Bs*) and sternellum (*Sl*) by a furcal suture (*k*) forming an internal furcal ridge between bases of sternal apophyses; the following intersternite has become a spinasternum (*Ss*) by union with segmental sternite; subcoxa (*Scx*) united ventrally with sternum.

D, typical definitive sternum, composed of primary sternite (*A, B, Stn*), a pair of subcoxal laterosternites (*Ls, Ls*), and the spinasternite (*Ss*); area of primary sternite divided into basisternum (*Bs*) and sternellum (*Sl*) by the furcal suture (*k*), and with a narrow presternum (*Ps*) set off by a secondary presternal suture (*j*).

inflection of the sternal wall. In this way is formed the typical, forked endosternal structure known as the *furca*, the evolution of which has been portrayed by Weber (1928). The part of the sternum bearing the furca lies between the coxae, and is usually much narrowed by comparison with the region of the sternum anterior to it.

The definitive sternal plate, whether it includes subcoxal laterosternal elements and the following intersternite, or does not, is commonly subdivided into an anterior and a posterior region. Fundamentally the



dividing line is a transverse inflection, or "suture," passing through the bases of the sternal apophyses (fig. 18 C, *k*). The inflection is usually strongly sclerotized, forming an internal ridge evidently designed to brace the sternum and to support the apophyses (figs. 21 B, 31, *k*); it sometimes remains weak, however, and establishes a line of flexibility in the sternum. In either case the sternum is demarked by the furcal ridge and its suture (*k*) into a *prefurcal area* (fig. 18 C, *Bs*) and into a *postfurcal area* (*Sl*).

The anterior region of the sternum has been variously named *sternum*, in a restricted sense, *antesternum*, *mesosternum*, *basisternum*, *eusternum*, and *sternannum*; the second has been called *sternellum*, *poststernum*, *metasternum*, and *furcasternum*. There are objections to all but one of these terms. "Antesternum" and "poststernum" (Amans, 1885) are applicable in some cases, but there is often a pre-sternal piece before the "antesternum," and very commonly the intersegmental spina-bearing plate forms an actual poststernal element of the definitive sternum behind the "poststernum." "Mesosternum" and "metasternum" (Berlese, 1909) violate the priority of the segmental prefixes. "Basisternum" and "furcasternum" (Crampton, 1909) are misleading because the part designated by the first is not basal, and that bearing the second name does not always carry the furcal apophyses. "Eusternum" (Snodgrass, 1910) implies that the part so named is the "true" sternum, which it is not. "Sternannum" (Mac Gillivray, 1923) has no grammatical standing, so far as the writer can find. "Sternellum" (MacLeay, 1830) alone can be given a clean bill. Of the terms applied to the prefurcal area, however, "basisternum" appears to be the least objectionable. In the present paper, therefore, the writer adopts the following terms for the principal divisions of the definitive sternum (fig. 18 D): *presternum* (*Ps*), *basisternum* (*Bs*), *sternellum* (*Sl*), and *spinasternum* (*Ss*). The first three are secondary subdivisions of the primary segmental sternum; the fourth is the intersegmental intersternite. To the primary sternal region there may be added on each side a subcoxal *laterosternite* (*Ls*).

The parts of the definitive thoracic sternum as described here fit exactly with the definitions of the sternal sclerites given by Weber (1928, pp. 250, 251), with the understanding that the term "sternellum" is substituted for "furcasternum," and that the poststernite is the intersegmental spinasternite. This idea of the sternal composition differs from Crampton's (1909) conception in that the fundamental transverse dividing line of the sternum is assumed to be the furcal suture (*k*) between the bases of the sternal apophyses, and not a divi-

sion anterior to the apophyses. A prefurcal division sometimes does occur (fig. 17, *l*), but it is clearly of a secondary nature and is variously produced.

The furcal suture is subject to much diversity in form, being sometimes produced forward and branched laterally, or curved posteriorly, thus giving a variety of structure to its apodemal ridge, and often obscuring the primary line of the sternal division.

The form and size of the sternal plates are frequently altered by a variation in the extent of the ventral sclerotization in the different thoracic segments. In the Blattidae it is evident that a partial desclerotization of the sternal cuticula has produced the unusual shapes and relationships of the sternal sclerites of the thorax (fig. 19). The prosternum most nearly preserves the typical form (B). It comprises two median plates (*A*, *Bs*<sub>1</sub>, *Sl*<sub>1</sub>) separated by a transverse fold (*k*) across the sternal region, from which arise the prosternal apophyses (*SA*<sub>1</sub>). A comparison with the assumed generalized structure of a thoracic sternum (B) will easily suggest that the transverse fold is the furcal suture (*k*), and that the pattern of the prosternal plates (C) has been produced by suppression of sclerotization in the lateral fields of the sternal area. In the mesothorax of *Blatta* (A) the ventral sclerotization is reduced to a pair of basisternal plates (*Bs*<sub>2</sub>), and a Y-shaped furca-bearing sclerite (*Sl*<sub>2</sub>), the two separated by an ample membranous area. In the latter are remnants of the sternal fold (*k*) from which arise the sternal apophyses (*SA*<sub>2</sub>) at the ends of the sternellar arms. The diagram D shows more clearly the relation of the mesosternal structure in the roach to the fundamental sternal structure (B), and again suggests that the peculiar features of the thoracic sterna of the roach are results merely of a reduction in the extent of the sclerotized areas. The metasternum of *Blatta* (A) is essentially the same as the mesosternum, but the sternal fold appears to be suppressed and the apophyses (*SA*<sub>3</sub>) arise from the sternellum (*Sl*<sub>3</sub>).

In some insects a thoracic sternum may be divided into two parts by a suture that is quite independent of the furcal suture. A clear case of this is seen in the thorax of the large embiid *Cylindrachaeta* (fig. 17), where a suture (*l*) cuts the mesosternum into an anterior plate (*1S*<sub>2</sub>) and a posterior plate (*2S*<sub>2</sub>). The second plate is marked by the usual furcal suture (*k*) and bears the furcal arms; it is a true furca-sternite. The metasternum has the usual structure, though the sternellum is reduced to a narrow band behind the furcal suture (*k*).

Most entomologists have believed that the sternum of a thoracic segment of an insect is "composed of" two principal plates, and the

pattern of the sternal sclerites in the cockroach (fig. 19) has had much to do with establishing this idea, for students have not recognized that the separated plates here are products of sclerotic degeneration, and that the fundamental structure, as shown best in the prothorax, is the same as in insects with undivided thoracic sterna. While the Blattidae undoubtedly retain some relatively generalized structural

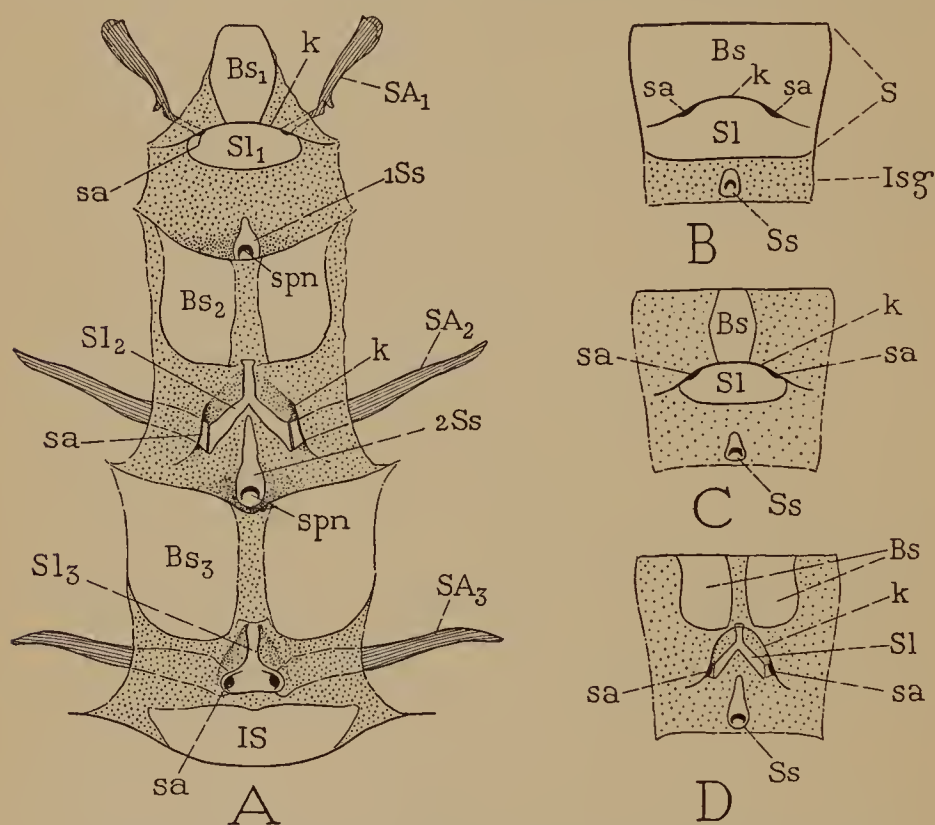


FIG. 19.—The thoracic sterna of a cockroach, *Blatta orientalis*.

A, general view of the three thoracic sterna and their paired apophyses. B, diagram of typical structure of a sternum. C, diagram of prosternum of *Blatta*. D, diagram of mesosternum of *Blatta*.

Bs, basisternum; IS, first abdominal sternum; k, furcal suture; SA, sternal apophysis; sa, external pit of sternal apophysis; Sl, sternellum; spn, external pit of spina; Ss, spinasternum; S, segmental sternum.

characters, they are in many respects highly specialized insects adapted to a particular kind of habitat, though to one almost universally distributed. The flattening of the body has been accompanied by a structural alteration in most of the under parts of the thorax, and there is every reason to believe that the sterna, covered as they are by the bases of the legs, have become largely membranized to allow of an inflection of their posterior parts. We should be on very unsafe ground, therefore, if we take the fragmented condition of the sternal sclerotization

in the thorax of the roach as representative of the primitive structure of the thoracic sterna in insects.

A search for a generalized thoracic sternum among all groups of insects, the writer believes, would reveal nowhere the thing sought for, because it does not exist. A study of the arthropods as a whole, however, suggests that the original area or areas of sclerotization in the ventral region of each segment spread into a continuous plate between the leg bases. The thoracic sterna of insects have been variously modified by the development of apodemal braces where rigidity is demanded, and by secondary divisions or by reductions in the areas of sclerotization where flexibility is important. This theory recommends itself by the fact that it permits all kinds of specific structures and sclerotic patterns to arise, and does not assume that homologies must exist where none can be established.

## II. THE THORACIC SKELETON OF DISSOSTEIRA

The Carolina locust, *Dissosteira carolina*, is here used as the subject for a special study of the thorax and its mechanisms because it is an insect sufficiently large for work on internal structure and is readily obtained, and because its muscular system is simple and comparatively easy to dissect. The thorax of the Acrididae is by no means generalized, but for this reason it offers a good test for the application of general principles to the solution of specific problems. The structural features of the thorax in the locust, however, are those common to all insects, and in the musculature there is almost no addition of special muscles such as are found in most of the higher insect orders and to some extent in the other orthopteran families.

The thorax of the jumping Orthoptera is so distinctly divided into a *prothorax* and a *pterothorax* that it is scarcely to be regarded as a unit in the organization of the body. The box-like structure of the combined mesothorax and metathorax, the oblique slant of the pleurites of these segments, and the firm connection of the first abdominal segment with the metathorax are characters evidently correlated with the development of the hind legs as saltatorial organs.

### THE CERVICAL SCLERITES

The grasshopper ordinarily keeps its head retracted against the prothorax, in which position the insect appears to have no neck, for the ample neck membrane (fig. 20 B, *Cv*), as well as the back part of the head, is thus concealed within the projecting anterior rim of the pronotum.



The neck skeleton of *Dissosteira* consists of two pairs of small *cervical sclerites* situated ventro-laterally in the membranous walls of the neck (fig. 20 B, *1cv*, *2cv*). The two sclerites of each pair in the grasshopper are closely hinged to each other, and form a bridge on each side between the head and the prothorax. The first sclerite (*1cv*) is an irregularly triangular plate articulating with the occipital condyle (fig. 32, *g*) of the posterior rim of the head, situated just above the base of the posterior tentorial arm (A, *PT*). Immediately behind its articulation this plate bears externally two small lobes that are conspicuous by their covering of short hairs. The second cervical sclerite (fig. 20, B, *2cv*) is a slender bar articulating posteriorly with the anterior margin of the prothoracic episternum (*Eps*) just within the overlapping edge of the protergum. The two cervical sclerites of each pair are movably hinged to each other at an angle directed ventrally. They are mostly concealed when the head is in the usual retracted position, but they form a small prominence of the neck projecting just behind the base of the maxilla. The probable function and mechanism of the cervical sclerites will be described in connection with the account of the muscles inserted upon them.

The lateral, muscle-bearing cervical sclerites are probably homologous structures in all insects in which they occur. Dorsal and ventral neck plates are present in some insects, but they are variable in size and arrangement and are probably secondary sclerotizations of the neck membrane.

#### THE PROTHORAX

The prothorax of the grasshopper is a highly individualized segment of the body, for, though its posterior dorsal and lateral parts widely overlap the anterior part of the mesothorax, it is separated from the latter by an ample intersegmental membrane (fig. 20 B, *Mb*).

The external parts of the prothorax comprise tergal, pleural, and sternal sclerites. The principal plate is the tergum, a large bonnet-like piece that covers the back and most of the sides of the segment (fig. 20 A, *T*). Only a corner of each pleuron shows externally: this is the small triangular lobe lying anteriorly between the base of the leg and the lower margin of the tergum (fig. 20 A, *Eps*). The rest of the pleuron is deeply invaginated within the lateral wall of the tergum (B, *Eps*). The prosternum consists of two sclerites in the ventral wall of the segment between the bases of the first legs (fig. 21 A, *S*, *Ss*), the anterior one connected by the precoxal bridges (*Acx*) with the pleura. The prothoracic legs appear to be inserted between the sternum and the lower edges of the tergum, but the lateral connections of



the legs are really with the inflected pleura covered by the tergal extensions. The procoxal cavities are "open" behind, that is, there are no postcoxal sclerotizations. Lying before the coxa of each leg in the articular membrane of the leg base is a small trochantal sclerite (fig. 20 A, *Tn*).

*The protergum.*—The tergum of the prothorax, besides covering the back and sides of its own segment, projects posteriorly over the dorsum of the mesothorax in a wide, triangular lobe which fits between the bases of the folded front wings. The top of the tergal bonnet

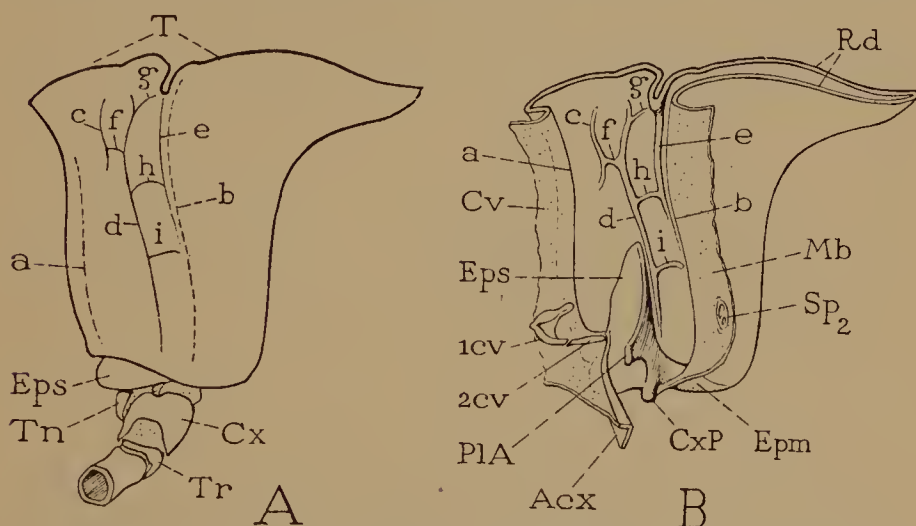


FIG. 20.—The prothoracic tergum and pleuron of *Dissosteira carolina*.

A, outer view of left side. B, inner view of right side, showing episternum invaginated within the tergum.

*a*, posterior edge of anterior fold of tergum; *b*, anterior edge of posterior fold (B, *Rd*) of tergum; *c*, *d*, *e*, the external vertical grooves or sutures of the tergum (A) forming the internal tergal ridges (B); *f*, *g*, *h*, *i*, horizontal sutures and their ridges connecting the vertical sutures and ridges.

(fig. 20 A, *T*) is cut by a deep transverse notch somewhat before the middle, and the part before the notch is compressed into a median ridge.

Each lateral area of the protergum is marked by a number of grooves forming a definite pattern, and by two non-impressed lines. The first non-impressed line (fig. 20 A, *a*) lies near the anterior border of the tergum and runs parallel with it; the second (*b*) extends downward in a sinuous course just posterior to the dorsal tergal notch. These two lines mark the limits of the inner folds of the anterior and posterior inflections of the tergal wall (B, *a*, *b*). The grooves of the tergal surface (A, *c-i*) lie in the space between the two non-impressed lines. They have no significance in themselves, but it is important to note

their positions because they form ridges on the inner surface (B) which have definite relations to the muscle attachments of the protergum. The first (*c*) is a short curved line on the upper lateral part of the tergum; the second (*d*) is a longer line extending from the back almost to the ventral margin of the tergum; the third (*e*) begins at the dorsal notch and reaches ventrally just before the second non-impressed line (*b*) to the middle of the side. Connecting the three vertical grooves are four short longitudinal grooves, one (*f*) lying between the first and second vertical grooves (*c, d*), the other three (*g, h, i*) between the second and third vertical grooves (*d, e*).

A study of the inner surface of the tergum (fig. 20 B) will show the endoskeletal ridges (*c-i*) formed by the external grooves. There

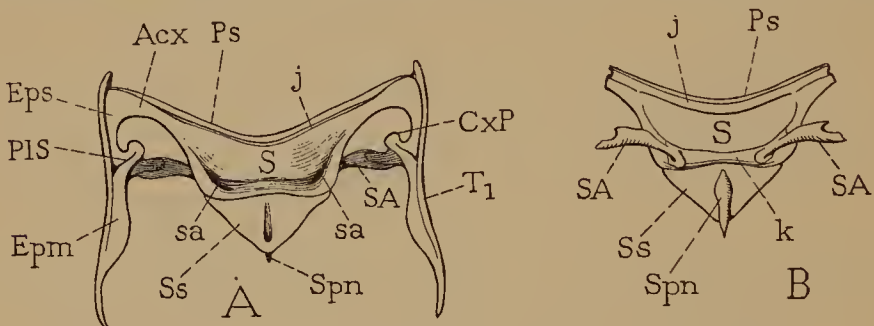


FIG. 21.—The prothoracic sternum and pleura of *Dissosteira*.

A, ventral view of sternum and lower edges of pleura, showing the spina-sternum (*Ss*) united with the segmental sternal plate (*S*), the latter continuous with the episterna (*Eps*) by the antecoxal bridges (*Acx*). B, dorsal surface of sternum, showing bases of sternal apophyses (*SA, SA*) united by a furcal ridge (*k*).

will also be noted the anterior and posterior inflections of the tergal walls. From the margin of the first inflection (*a*) the neck membrane (*Cv*) is reflected forward, and from the margin (*b*) of the posterior fold or reduplication (*Rd*) the intersegmental membrane (*Mb*) is reflected posteriorly to the mesothorax. The first spiracle (*Sp<sub>2</sub>*) is located in this membrane.

*The propleura.*—We have already noted that each pleuron of the prothorax appears externally only as a small plate projecting from beneath the edge of the tergum anterior to the base of the leg (fig. 20 A, *Eps*). It is to be seen on the internal surface of either half of the segment (B), however, that the pleural piece exposed externally is merely the lower anterior corner of a much larger triangular sclerite (B, *Eps*) extended upward within the lateral tergal wall by a deep inflection of the tergo-pleural membrane. The posterior margin of the sclerite is turned inward, forming the pleural ridge, which gives off

the pleural arm (*PLA*) and ends ventrally in the articular process of the coxa (*CxP*). Behind the lower part of the pleural ridge is a small epimeral piece (*Epm*) fused with the lower border of the tergum and concealed just within the edge of the latter. The anterior ventral angle of the episternum is continuous through the precoxal bridge (*Acx*) with the anterior lateral angle of the prosternum (fig. 21 A).

*The prosternum.*—The sternum of the prothorax in the grasshopper consists of two distinct plates (fig. 21 A, *S*, *Ss*) separated by a transverse suture. The anterior plate (*S*) is the larger and the more strongly sclerotized. It is continuous laterally with the precoxal bridges (*Acx*) from the episterna (*Eps*). The definitive sternal plate of the prothorax, then, evidently includes laterosternal elements derived from the pleura (subcoxae), but the true pleuro-sternal limits are entirely obliterated. The anterior rim of the sternum is set off as a narrow presternal strip (*Ps*) by a submarginal external suture (*A*, *j*) and a corresponding internal ridge (*B*, *j*). Posteriorly the first sternal plate is marked by a deep transverse groove which forms a strong ridge on its inner surface (fig. 21 B, *k*) between the bases of the sternal apophyses (*B*, *SA*, *SA*), which latter are indicated externally by a pair of pits (*A*, *sa*, *sa*). The first prosternal plate in the grasshopper, therefore, is divided in the primitive fashion (fig. 18 C) into a basisternal and a sternellar region by the suture of a ridge connecting the bases of the apophyses. The prosternal apophyses are simple arms (fig. 21 B, *SA*) diverging dorsally and laterally. Their distal ends are solidly united with the corresponding pleural apophyses.

The second prosternal plate (fig. 21, *Ss*) is a spinasternite, and is, therefore, the intersternite between the prothorax and the mesothorax which has become closely associated with the primary sternite of the prothorax. It is mostly overlapped by the anterior margin of the mesosternum. The spinasternite of *Dissosteira* is triangular in shape, and is marked by a deep median impression (fig. 21 A) which forms the spina internally (*B*, *Spn*).

#### THE PTEROTHORAX

The united mesothorax and metathorax of the grasshopper constitute a unit in the body mechanism. The pleural and sternal walls of the two segments are solidly united, forming a trough-like structure perforated only by the openings of the coxal cavities. The leaping force of the hind legs is thus applied to a rigid middle section of the body, which also bears the wings. The dorsum of this body section is covered by the mesothoracic and metathoracic terga, but these plates

are freely attached to the upper pleural margins of the pterothoracic trough by the ample membranes of the wing bases, and they are movably joined to each other. As we shall later see, the wing mechanism demands at least a limited freedom of movement in the wing-bearing terga.

In the grasshopper the back plates of the pterothorax (figs. 22, 24) differ somewhat in shape and in details of form and proportion, but the two have the same essential structure. They are relatively small, and when the insect is at rest they are hidden beneath the folded wings. The pleurites are defined externally by distinct grooves (fig. 26) forming strong ridges internally (fig. 28), which slant posteriorly and downward in a manner to suggest that they serve thus to brace the pleural walls against the projectile force of the hind legs. The sterna of the wing-bearing segments are wide plates fused laterally with the pleura before the leg bases (fig. 30).

*The mesotergum.*—The tergum of the mesothorax (fig. 22 A) is a rectangular plate ending posteriorly in a distinct, transverse fold (*Rd*), the extremities of which are continued into the posterior thickened margins, or axillary cords (*Arc*), of the wing bases. Close to the anterior margin of the tergum is a deep groove (*acs*). This is the antecostal suture, or primary intersegmental inflection which forms the antecosta of the internal surface of the definitive tergum (*B*, *Ac*). The antecosta bears laterally two wide, flat apodemal plates (*lPh*) projecting into the cavity of the thorax (fig. 25), which are the first pair of thoracic phragmata.

On the external surface of the mesotergum, two sutures (fig. 22 A, *ps*, *ps*) diverge laterally and posteriorly from the antecostal suture (*acs*). They form internally a pair of strong ridges (*B*, *PR*) extending to the bases of the anterior wing processes (*ANP*). The large, irregular, triangular regions (*A*, *Psc*, *Psc*) forming the anterior lateral angles of the tergum, set off by the divergent sutures (*ps*, *ps*), constitute the prescutal areas of the tergum. In the metathorax the prescutal sutures do not meet the antecostal suture, and the lateral prescutal lobes are continuous by a narrow median bridge behind the antecostal suture (fig. 24). In some other Acrididae, as in *Melanoplus*, the continuity of the prescutal area is more pronounced. In other orthopteran families the prescutum is narrow, but in the Blattidae and Gryllidae there is a suggestion of its separation from the scutal area. In any case, however, the prescutum of the Orthoptera must be regarded as a secondary differentiation of the anterior part of the tergum. Its lateral parts become most sharply defined in the mesotergum of the Acrididae by the strong development of the prescutal ridges (fig.



22 B, *PR*) that brace the anterior wing processes. Upon the irregular surfaces of the prescutal lobes are attached the tergo-sternal muscles which are the principal elevators of the wings.

A prescutum similar to that of the Orthoptera occurs also in certain other insects, though very likely it may be an independent differentiation formed as an adaptation to similar demands. In many insects of the higher orders, however, such as the Hemiptera, Diptera, and Hymenoptera, a prescutal area of quite a different nature is set off in the anterior median part of the tergum by the development of two

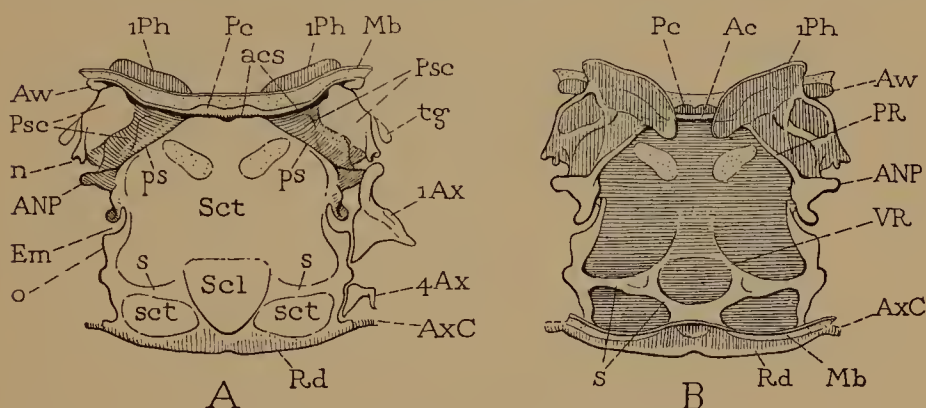


FIG. 22.—The mesothoracic tergum of *Dissosteira*.

A, dorsal surface. B, ventral surface. *Ac*, antecosta; *acs*, antecostal suture; *ANP*, anterior notal wing process; *Aw*, prealar arm of tergum; *1Ax*, first axillary; *4Ax*, fourth axillary; *AxC*, axillary cord; *Em*, lateral emargination of tergum; *Mb*, secondary intersegmental membranes; *n*, lobe of prescutum articulating with base of subcostal wing vein; *o*, lobe of scutum articulating with posterior part of first axillary; *Pc*, precosta; *1Ph*, first phragma; *ps*, prescutal suture; *Psc*, *Psc*, lateral prescutal areas; *Rd*, posterior reduplication of tergum; *Scl*, scutellum; *Sct*, principal part of scutum; *sct*, *sct*, posterior lateral subdivisions of scutum; *s*, *s*, secondary ridges of tergum; *tg*, tegular rudiment; *VR*, remnant of V-ridge of tergum.

lateral ridges, the parapsidal gradients (fig. 5 B, *PaR*), which extend a varying distance posteriorly from the anterior tergal margin, and usually converge. These ridges and their sutures apparently lie in the scutal region of the tergum, for there is sometimes present a narrow transverse prescutal band anterior to their bases. Parapsidal ridges are absent in the Orthoptera.

The area of the mesotergum of *Dissosteira* posterior to the antecostal and prescutal sutures is differentiated topographically into a large anterior scutal region (fig. 22 A, *Sct*), a median, posterior, triangular scutellar region (*Scl*), two small, lateral, posterior scutal regions (*sct*, *sct*), and a posteriormost, deflected marginal region (*Rd*). The structure here presented is quite different in appearance from that of a typical wing-bearing tergum (fig. 5 A) in which the surface

is divided into scutal and scutellar areas (*Sct*, *Scl*) by the suture (*vs*) of an internal V-shaped ridge (*B*, *VR*), the arms of which are convergent forward from the posterior lateral angles of the tergum.

In the Acrididae the V-shaped endotergal ridge (fig. 22 *B*, *VR*) is almost obliterated, and the tergum is braced by two secondary ridges, one on each side (*s*), that converge posteriorly from the posterior lateral margins of the scutal area and intercept the arms of the rudimentary V-ridge (*VR*). The altered structure of the acridid tergum

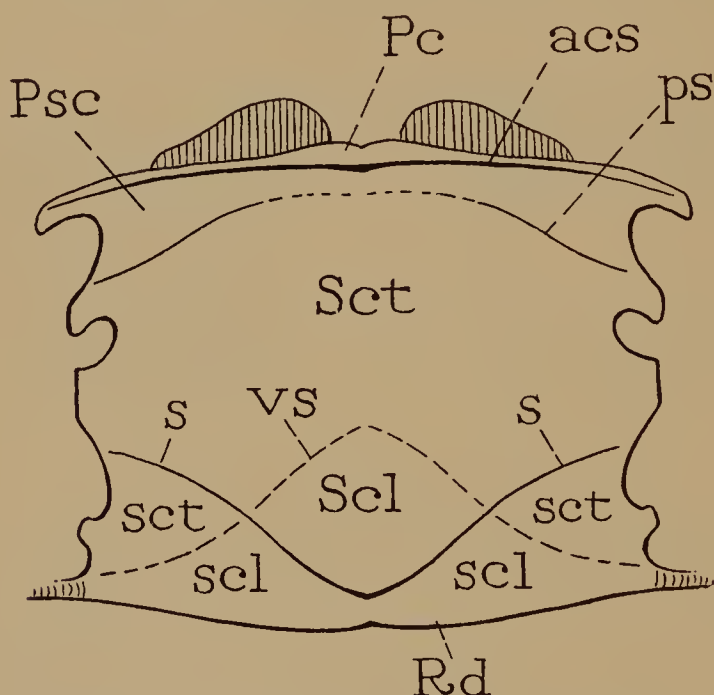


FIG. 23.—Diagram of the structure of a wing-bearing tergum of Acrididae.

The prescutal suture (*ps*) is either continuous, or suppressed medially; the usual V-ridge and its suture (*vs*) are partially suppressed and subordinated to a secondary ridge of similar shape but having its arms (*s*, *s*) convergent posteriorly.

may be expressed diagrammatically as in figure 23, where the suppressed suture (*vs*) of the obsolete V-ridge is crossed by the dominant suture (*s*) of a secondary ridge of similar shape but having its arms convergent posteriorly. Thus the scutum consists of a principal anterior scutal area (*Sct*) and of two small postero-lateral scutal areas (*sct*, *sct*); and the scutellum is divided into a median scutellar area (*Scl*) and two lateral scutellar areas (*scl*, *scl*), including the posterior fold of the tergum (*Rd*). The evolution of this condition can be traced in other Orthoptera from the primary structure which occurs in the Blattidae. A similar modification has taken place in the mesotergum of Hemiptera and Coleoptera, producing the triangular elevated shield of the scutellum that lies between the bases of the folded wings.

It is clear that the external "divisions" of the wing-bearing tergum are incidental to the development of the internal ridges, which are adaptations to the part the tergum plays in the mechanism for moving the wings. The old idea that the tergum is "composed of" sclerites gave undue emphasis to surface features. Though a study of the latter may have a value for descriptive purposes, the student must look to the internal characters for a true understanding of the skeleton of insects.

There is no postscutellar plate in the mesothorax of the grasshopper. The posterior deflected margin of the scutellum ends in a narrow intersegmental membrane (fig. 25, *2Mb*) uniting the mesotergum with the anterior margin of the precosta of the metatergum. The tergum of the mesothorax of the grasshopper, therefore, is a typical dorsal plate of a secondary segment, comprising the primary segmental sclerotization and the preceding primary intersegmental sclerotization of the back. In the latter the primary intersegmental fold is marked by the antecosta (fig. 25, *Ac*) and the antecostal suture (*acs*).

The lateral margins of the mesotergum are very irregular (fig. 22). The wings are extended from the tergal edges between the middle of the prescutal borders and the posterior reduplication of the scutellum. Anterior to the wing bases the anterior angles of the tergum are extended as short prealar arms (fig. 22 *A*, *Aw*) to which are articulated the dorsal processes of the first basalar plates (fig. 26, *Ba*). The lateral margin of the prescutal area forms posteriorly a small process bearing a socket-like surface (*n*) in which the base of the subcostal wing vein turns when the wing is flexed or extended. Posterior to this process the anterior angle of the scutum is produced to form the large *anterior notal wing processes* (*ANP*), which support the neck of the first axillary sclerite of the wing base (*1Ax*). The inner edge of the first axillary bridges the *lateral emargination* of the tergum (*Em*) and articulates with a marginal lobe (*o*) behind the latter. There is no posterior notal wing process in the mesotergum of the grasshopper; the fourth axillary (*4Ax*), which is itself probably a detached piece of the tergal margin, articulates with the edge of the scutellum.

*The metatergum.*—The tergal plate of the metathorax (fig. 24) is somewhat longer than that of the mesothorax, since it must support the wider bases of the hind wings; but in many respects it is more weakly developed than the mesotergum, there being extensive non-sclerotized areas in the posterior part of the scutal region.

The precostal rim of the metatergum (fig. 24, *Pc*) is narrow, except medially where it forms a conspicuous lip before the deeply inflected

antecostal suture (*acs*). The prescutal ridges and their sutures (*ps*, *ps*) are much weaker than those of the mesotergum, but they are not confluent medially with the antecostal ridge and suture, and the lateral prescutal triangles (*Psc*, *Psc*) appear to be continuous across the back in a narrow, weakly sclerotized area deflected into the antecostal suture (*acs*).

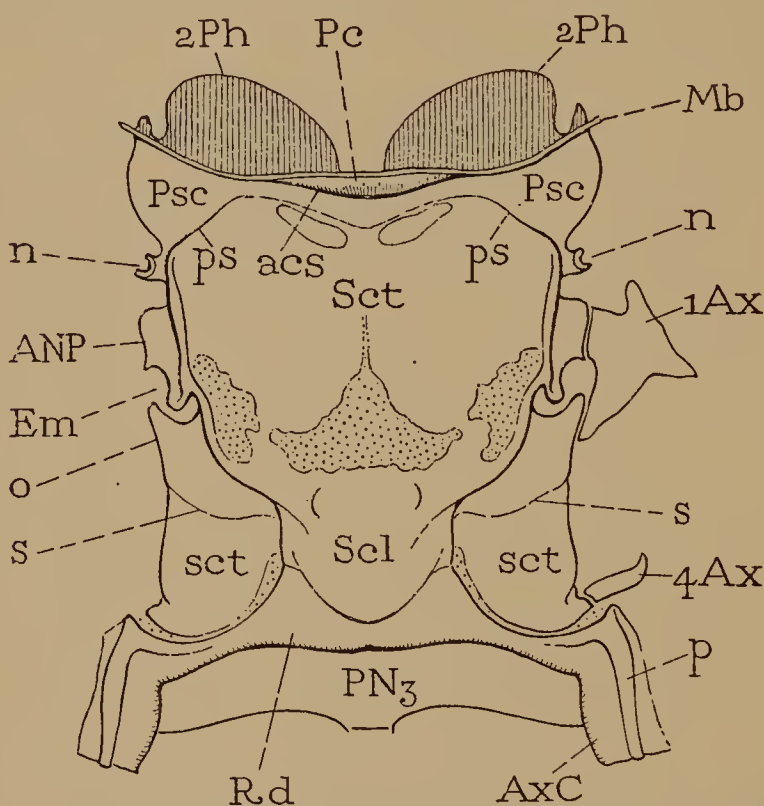


FIG. 24.—The metathoracic tergum and postnotal plate of *Dissosteira*.

*acs*, antecostal suture; *ANP*, anterior notal wing process; *1Ax*, first axillary; *4Ax*, fourth axillary; *AxC*, axillary cord; *Em*, lateral emargination of tergum; *n*, prescutal lobe to which base of subcostal wing vein is attached; *o*, tergal lobe to which posterior end of first axillary articulates; *p*, tergal arm supporting anal veins of wing (see fig. 47 B); *Pc*, precosta; *2Ph*, second phragma; *PN<sub>3</sub>*, postnotum; *ps*, prescutal suture; *Psc*, prescutum; *Rd*, posterior fold of tergum (see fig. 25, *Rd<sub>a</sub>*); *s*, *s*, sutures of secondary tergal ridges; *Scl*, scutellum; *Sct*, principal part of scutum; *sct*, *sct*, subdivisions of scutum.

The surface features of the scutal and scutellar regions of the metathoracic tergum have even less relation to the generalized structure of a wing-bearing tergum than do those of the mesotergum, because the tergal ridges (fig. 23) are here almost completely suppressed, and the external characters are the result of secondary inflections which produce a topographical pattern quite independent of the primary divisions of the tergum (fig. 5). Most of the scutal region (fig. 24, *Sct*) and the



median triangle of the scutellar region (*Scl*) are confluent in a large shield-shaped area that forms the principal part of the tergal plate. The depressed posterior lateral parts of the scutum (*sct*, *sct*) are cut transversely by the faintly-marked sutures (*s*, *s*) of the posteriorly convergent ridges, which are obsolete in the metatergum, though strongly developed on the mesotergum (fig. 22 B, *s*). The posterior marginal area of the metatergum (fig. 24, *Rd*), which is a part of the true scutellar region, is sharply inflected (fig. 25, *Rd*<sub>3</sub>) and is continuous with the greatly extended precosta of the first abdominal segment, which constitutes a postnotal plate of the metathorax (figs. 24, 25, *PN*<sub>3</sub>).

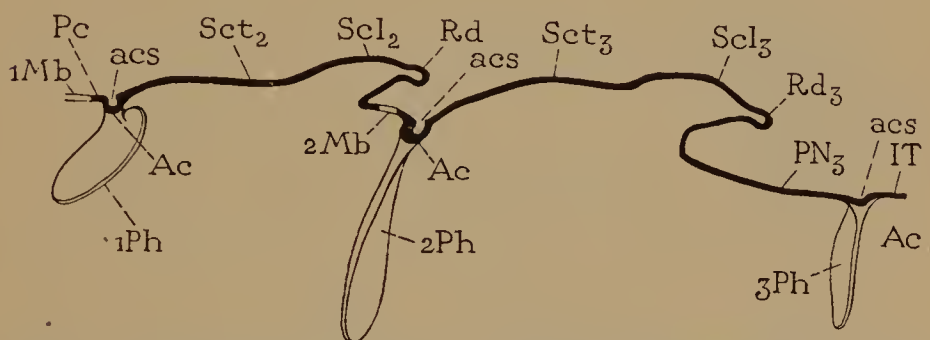


FIG. 25.—Median longitudinal section of mesotergum, metatergum, and meta-thoracic postnotal plate of *Dissosteira*, showing the phragmatal lobes of the right side.

*Ac*, antecosta; *acs*, antecostal suture; *IT*, first abdominal tergum; *1Mb*, *2Mb*, secondary intersegmental membranes; *1Ph*, *2Ph*, *3Ph*, first, second, and third phragmata; *PN*<sub>3</sub>, postnotal plate of metathorax, or greatly enlarged precosta of first abdominal tergum; *Rd*, posterior reduplication of tergum; *Sct*, scutum; *Scl*, scutellum.

The lateral margins of the metatergum present the same features as do those of the mesotergum. The posterior angle of each prescutal area projects as a small marginal process (fig. 24, *n*) which is connected with the head of the subcostal wing vein by a ligament-like thickening of the basal wing membrane; it does not articulate with the vein as in the mesothorax. The anterior notal wing process (*ANP*) is a flat lobe of the scutum, to which the first axillary (*1Ax*) is closely hinged. Behind the wing process is a deep emargination (*Em*) of the scutellum, posterior to which is a second lobe (*o*) articulating with the posterior end of the first axillary. The slender fourth axillary (*4Ax*) articulates with the extreme posterior angle of the lateral scutellar area (*sct*). Each extremity of the posterior marginal fold of the tergum (*Rd*) gives off into the anal membrane of the wing a long arm (*p*) that supports the anal veins (fig. 47 B).

*The pterothoracic pleura.*—The pleurites of each side of the mesothorax and metathorax are firmly united to form continuous lateral walls of the pterothoracic region (fig. 26) in which the episterna and epimera (*Eps*, *Epm*) are distinct plates separated by oblique grooves sloping from above downward and posteriorly. The first principal groove is the pleural suture of the mesothorax (*PLS*<sub>2</sub>), the second is the intersegmental line, the third is the pleural suture of the metathorax (*PLS*<sub>3</sub>). Each pleural suture terminates above in a large wing

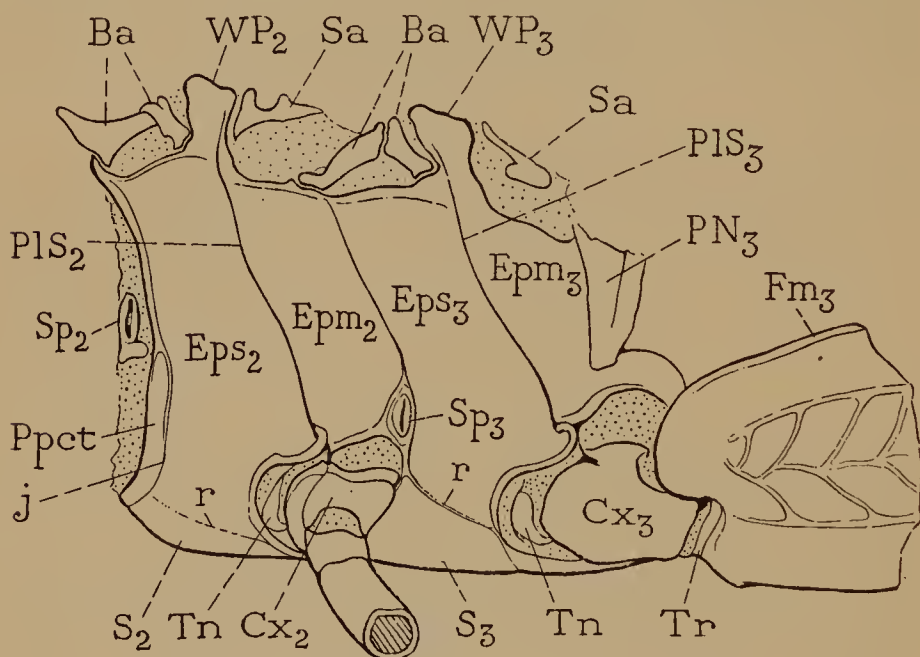


FIG. 26.—The pterothoracic pleura of *Dissosteira*.

*Ba*, basalar sclerites; *Cx*, coxa; *Epm*, epimeron; *Eps*, episternum; *Fm*<sub>3</sub>, base of hind femur; *j*, prepectal suture; *PLS*, pleural suture; *PN*<sub>3</sub>, lateral arm of metathoracic postnotum; *Ppct*, prepectus; *r*, pleuro-sternal suture; *S*, sternum; *Sa*, subalare; *Sp*<sub>2</sub>, mesothoracic spiracle; *Sp*<sub>3</sub>, metathoracic spiracle; *Tn*, trochantin; *Tr*, trochanter; *WP*, pleural wing process.

process (*WP*<sub>2</sub>, *WP*<sub>3</sub>), and below in the pleural articulation of the coxa. The episternum of each segment (*Eps*<sub>2</sub>, *Eps*<sub>3</sub>) is united ventrally before the coxal cavity with the edge of the sternum, the line of union (*r*) in the adult insect being obsolete in the mesothorax, but distinct in the metathorax. In the nymph of *Dissosteira* and of other Acrididae (fig. 27 A) the ventral edge of the precoxal part of the pleuron in both the mesothorax and the metathorax is distinctly separated from the sternum; in the nymph of *Gryllus* (B) a precoxal plate (*Acx*) is separated from the pleuron and intervenes between the episternum and the sternum. The episternum of the mesothorax of *Dissosteira* (fig. 26, *Eps*<sub>2</sub>) is marked anteriorly by a submarginal

suture ( $j$ ) which is continuous through the anterior part of the mesosternum ( $S_2$ ) and sets off from the sternum and the two episterna a narrow anterior marginal piece, or *prepectus* ( $Ppct$ ), which is analogous to the similar sclerite of the Ichneumonidae and some other Hymenoptera. To the posterior margin of the epimeron of the metathorax ( $Epm_3$ ) is attached the large lateral extension of the metathoracic postnotum ( $PN_3$ ).

The two pairs of spiracles of the thorax are presumably the mesothoracic spiracles and the metathoracic spiracles, each pair being displaced anteriorly. The first spiracle on each side (fig. 26,  $Sp_2$ ) is

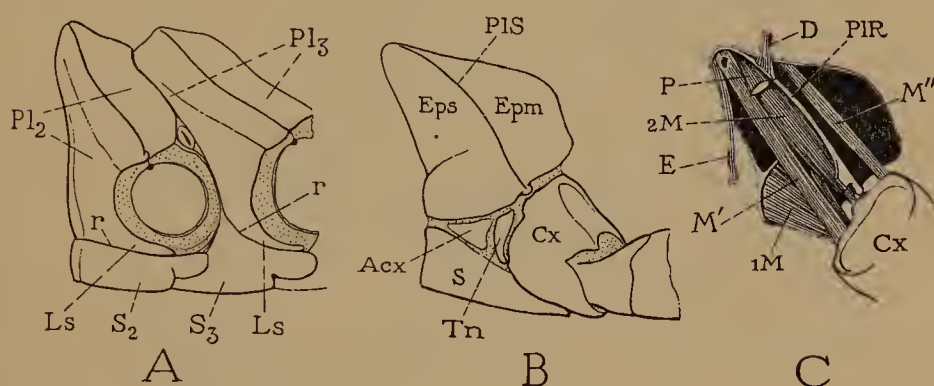


FIG. 27.—Pterothoracic pleura of orthopteran nymphs.

A, pterothoracic pleura of an acridid nymph, showing laterosternal arms of pleura ( $Ls$ ) separated from sternum ( $S_2$ ,  $S_3$ ) by the pleuro-sternal sutures ( $r$ ,  $r$ ).

B, mesopleuron and coxa of young nymph of *Gryllus assimilis*, showing a distinct precoxal sclerite ( $Acx$ ) between episternum ( $Eps$ ) and sternum ( $S$ ). C, inner view of B, showing the basalar and subalar muscles of the nymph ( $M'$ ,  $M''$ ) attached dorsally on edges of episternum and epimeron, respectively.

situated laterally in the intersegmental membrane between the prothorax and the mesothorax, where it is covered by the posterior fold of the protergum. The second spiracle (fig. 26,  $Sp_3$ ) appears in the adult to lie in the lower posterior angle of the mesepimeron ( $Epm_2$ ) just above the base of the middle leg, and anterior to the fold between the mesothorax and the metathorax (fig. 28), but in the nymph (fig. 27 A) it occurs in the intersegmental fold.

The structural pattern of the internal surface of the pleural wall of the pterothorax (fig. 28) is a replica of that of the outer surface, except that the impressed lines of the latter are represented by ridges. Each pleural ridge ( $PIR_2$ ,  $PIR_3$ ), however, gives off from its lower end a large pleural arm, or pleural apophysis ( $PIA_2$ ,  $PIA_3$ ), that projects inward across the coxal cavity, where it is closely associated with the lateral arm of the corresponding sternal apophysis (fig. 31,

*PLA*, *SA*), and the two are connected by a dense mass of short muscle fibers (figs. 34, 35, 86, 115).

Of particular interest in the pterothoracic pleuron are the *epipleurites*, or the small plates situated in the membranes below the bases of the wings (figs. 26, 28, 29, *Ba*, *Sa*). Upon these plates are inserted the principal so-called *direct* muscles of the wing mechanism. In the grasshopper there are three epipleurites in each segment, two (*Ba*)

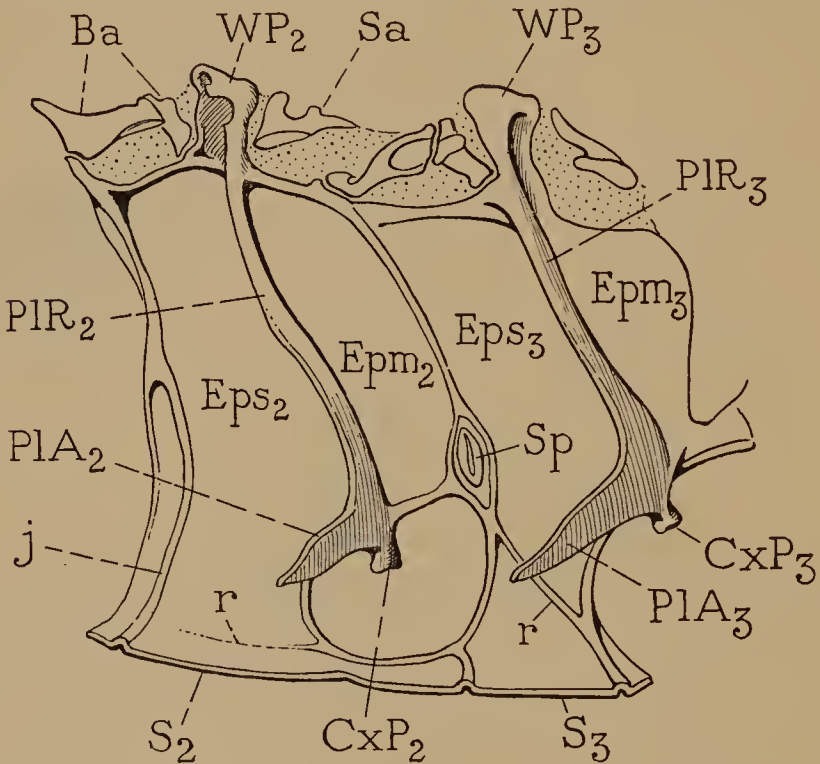


FIG. 28.—Inner surface of right pterothoracic pleura of *Dissosteira*, showing the endoskeletal features.

Lettering as on figure 26, with the following additions: *CxP*, pleural coxal process; *PLA*, pleural arm; *PIR*, pleural ridge.

situated before the wing process and articulated to the episternum, and one (*Sa*) in the membrane behind the wing process and above the epimeron. The episternal epipleurites are distinguished as the *basalares*, or *basalar sclerites* (*Ba*), the epimeral epipleurite as the *subalare* or *subalar sclerite* (*Sa*). In most insects there is but a single basalar. In *Dissosteira* the basalar sclerites are freely hinged to the upper margin of the episternum before the wing process (fig. 29, 1*Ba*, 2*Ba*) so that they can be turned inward and downward by the muscle inserted on their inner faces (fig. 49, *E*, *M'*). The function of the epipleurites in connection with the movement of the wings will be described in Section V.



There can be little doubt that the epipleurites are derived from the upper parts of the pleura. In a nymphal orthopteron the muscles that are inserted on the epipleurites in the adult (fig. 49) are attached directly to the upper edges of the episternum and epimeron (fig. 27 C, *M'*, *M''*). In many adult insects the basalar remains as an undetached lobe of the episternum (fig. 14 A, *Ba*).

In the membranous corium at the base of each leg there is a small plate (fig. 26, *Tn*) situated before the coxa and loosely attached by its lower end to the rim of the coxa. These sclerites are evidently remnants of the trochantins (fig. 13 A, B, *Tn*) since they exactly cor-

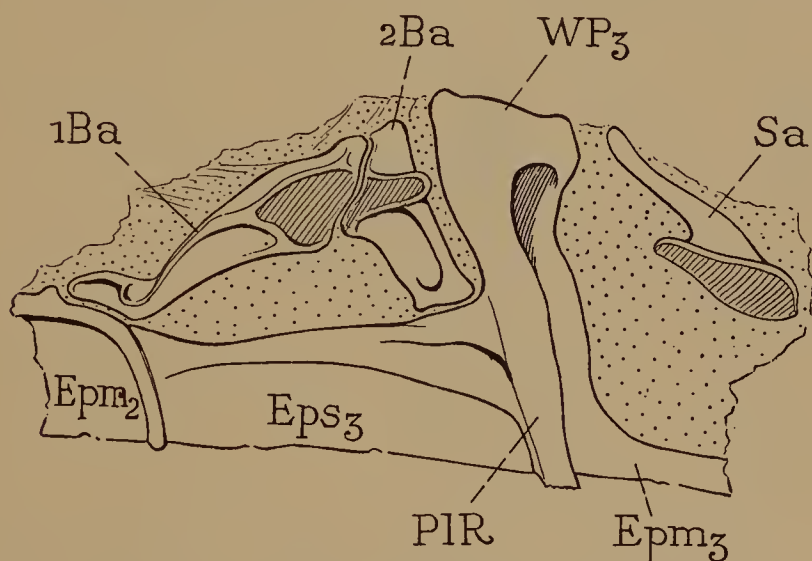


FIG. 29.—Upper edge of the metathoracic pleuron and epipleurites of *Dissosteira*, inner view.

*1Ba*, first basalar; *2Ba*, second basalar; *Epm*, epimeron; *Eps*, episternum; *Sa*, subalar; *WP*, pleural wing process.

respond with the small trochantin of the prothorax (fig. 20 A, *Tn*), which is identified as such by the attachment of the promotor leg muscle upon it (fig. 33 A, 62).

*The pterothoracic sterna.*—The sternal plates of the mesothorax and metathorax are united in a broad plastron covering the ventral surface of the pterothorax, and continuous laterally, in the adult, with the pleura by a fusion with the precoxal parts of the latter (fig. 30 A). In the nymph of *Dissosteira* and of other Acrididae, as already noted, the pleural plates of the mesothorax and metathorax (fig. 27 A, *Pl*<sub>2</sub>, *Pl*<sub>3</sub>) are distinctly separate from the sterna (*S*<sub>2</sub>, *S*<sub>3</sub>), and the precoxal part of each pleuron is extended ventrally and posteriorly as a slender arm (*Ls*, *Ls*) between the sternum and the coxal corium. These arms are clearly remnants of the infra-coxal arcs of the sub-

coxae (fig. 18 B). In the adult grasshopper they form the ventral rims of the coxal cavities, that of the mesothorax becoming a weakly sclerotized plate, that of the mesothorax a membranous fold. The definitive sterna of the pterothorax in the Acrididae, therefore, do not appear to contain subcoxal laterosternal elements as integral parts of their areas. In the adult of *Dissosteira* the pleuro-sternal suture (fig. 30 A, *r*) is obsolete in the mesothorax anterior to the coxa, but remains distinct in the metathorax.

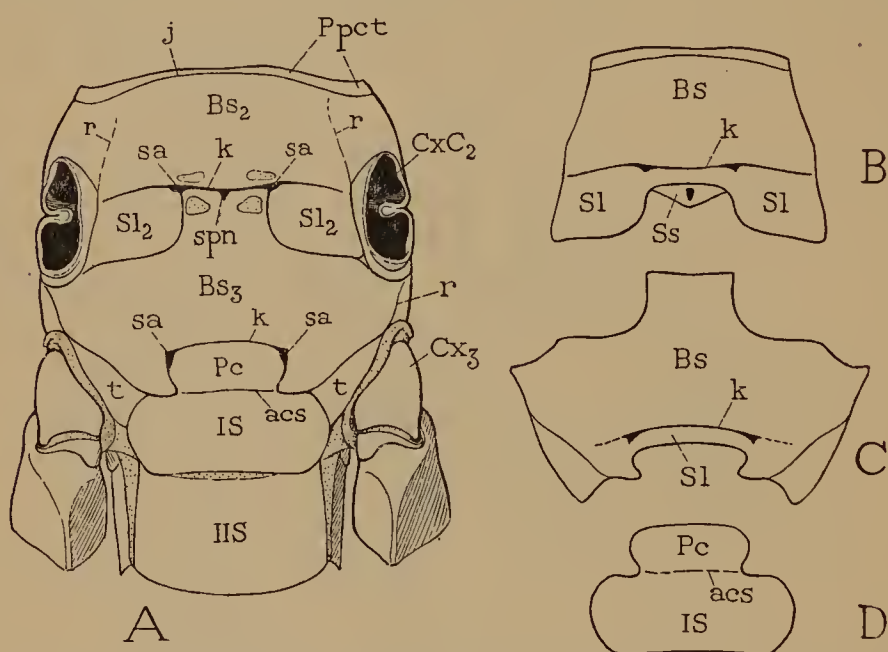


FIG. 30.—Pterothoracic sterna and the base of the abdomen of *Dissosteira*.

A, general view of pterothoracic sterna and first two abdominal sterna. B, diagram of probable structure of mesosternum. C, diagram of probable structure of metasternum. D, diagram of structure of first abdominal sternum.

*acs*, antecostal suture of first abdominal sternum; *Bs*, basisternum; *Cx*, coxa; *CxC*, coxal cavity; *IS*, *IIS*, first and second abdominal sterna; *j*, prepectal suture; *k*, furcal suture; *Pc*, precosta; *Ppct*, prepectus; *r*, *r*, pleuro-sternal sutures; *sa*, *sa*, roots of sternal apophyses; *Sl*, sternellum; *t*, *t*, infra-coxal lobes of metasternum.

The mesosternum of *Dissosteira* is a broad plate (fig. 30 A, *Bs<sub>2</sub>*, *Sl<sub>2</sub>*) bounded laterally by the obsolete lines of the pleuro-sternal sutures (*r*) and the rims of the coxal cavities. Its anterior edge is slightly convex; its posterior border is deeply emarginated to receive a median rectangular extension of the mesosternum (*Bs<sub>3</sub>*) which is dove-tailed into the mesosternal notch. A prominent transverse suture (*k*), which forms internally a ridge through the bases of the sternal apophyses and extends laterally toward the coxal cavities (fig. 31, *k*, *k*) is coincident with the posterior edge of the median part of the sternum and

contains the external impressions of the sternal apophyses (fig. 30 A, *sa*, *sa*). The suture, therefore, is the furcal suture of the mesosternum, and the two postero-lateral, quadrate mesosternal lobes (*Sl*<sub>2</sub>, *Sl*<sub>2</sub>) lying laterad of the median projection of the metasternum must belong to the sternellar region of the mesosternum. A median pit (*spn*) opening just behind the furcal suture (*k*) marks the site of the internal spina (fig. 31, *2Spn*), which normally is intersegmental between the mesosternum and the metasternum, but which is here fused with the mesosternal furcal ridge (*k*). There can be no doubt, therefore, that a part of the mesosternum normally intervening between the furcal ridge and the spinasternum, which is the median area of the mesosternellum (fig. 30 B, *Sl*), has been obliterated in *Dissosteira*, and that the spinasternum itself has been reduced to little more than the base of the spina.

The mesosternum of *Dissosteira* is thus to be analyzed into the same structural elements that are preserved in a less modified form in the prosternum. The sternellar region of the sternum (fig. 30 B, *Sl*, *Sl*) has been cut into a pair of lateral lobes (A, *Sl*<sub>2</sub>, *Sl*<sub>2</sub>) by the suppression of its median area, and the following spinasternum (B, *Ss*) has been reduced to the base of the spina (fig. 31, *2Spn*), which is united with the furcal ridge (*k*).

The endoskeletal features of the mesosternum consist principally of the strong furcal ridge (fig. 31, *k*, *k*) and the two sternal apophyses (*SA*, *SA*). The latter are broad, tapering plates arising from thick bases and extending laterally beneath the pleural apophyses, to which they are attached by short muscle fibers (figs. 34, 35, 86). Each has a triangular basal lobe directed forward. Anteriorly the mesosternum is marked by the sternal part of the prepectal ridge (fig. 31, *j*) which cuts off a marginal presternal strip continuous laterally with the pre-episternal areas of the prepectus (figs 26, 30, *Ppct*).

The metasternum of *Dissosteira* (fig. 30 A, *Bs*<sub>3</sub>) is wider than the mesosternum and is separated laterally by distinct sutures (*r*) from the precoxal parts of the metapleura. Its anterior margin, as just observed, is extended in a large, median, quadrate lobe which is dove-tailed between the scutellar lobes of the mesosternum. Its posterior edge is broadly emarginate to receive a corresponding extension of the first abdominal sternum (*Pc*). The median scutellar region of the metasternum, shown diagrammatically at C of figure 30, is suppressed in the same manner as is that of the mesosternum, and the suture of the transverse sternal ridge (*k*) is here also coincident with the transverse margin of the sternal notch; but the suture does not extend laterad of the apophyses (*sa*, *sa*), and the lateral sternellar lobes are, therefore,

not set off by sutures as in the mesosternum. The small triangular plates (*t*, *t*) bordering the coxal cavities appear to be subdivisions of the sternellar lobes rather than subcoxal laterosternal pieces, since the ventral arms of the pleurites in the nymph (fig. 27 A, *Ls*) form only the membranous folds beneath the coxal cavities in the metathorax.

There is no spina associated with the metasternum. Crampton (1918) says the spinal pit has disappeared from the metasternum, but he gives no evidence of its former existence. As we have seen, the intersternal sclerotization between the metasternum and the first abdominal sternum remains as an integral part of the latter, or disappears

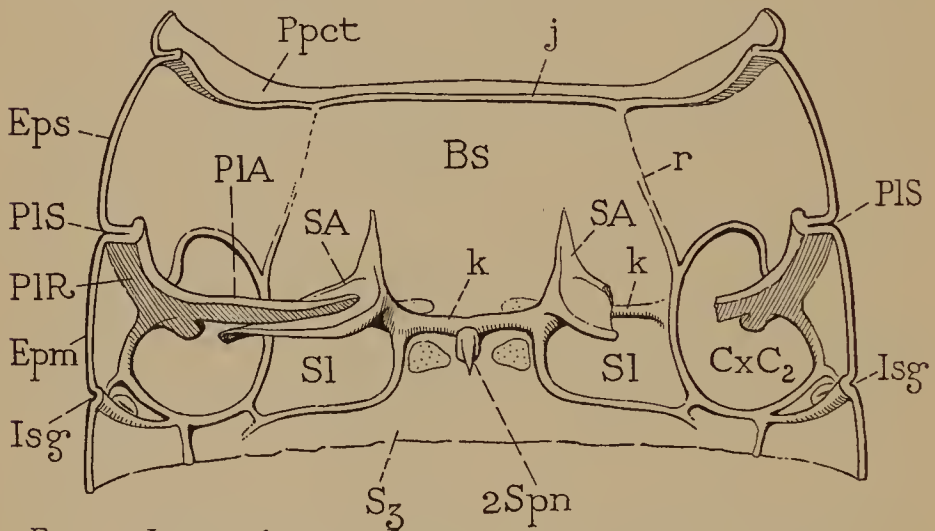


FIG. 31.—Inner surface of ventral pleuro-sternal region of mesothorax.

*Bs*, basisternum; *Cx C2*, coxal cavity; *Epm*, epimeron; *Eps*, episternum; *Isg*, intersegmental groove; *j*, ridge of prepectal suture; *k*, furcal ridge; *PIA*, pleural arm; *PIR*, pleural ridge; *PLS*, pleural suture; *Ppct*, prepectus; *S3*, anterior part of metasternum; *SA*, sternal apophysis; *Sl*, sternellum; *2Spn*, second spina, united with furcal ridge of mesosternum.

when the first abdominal sternum becomes rudimentary. In *Dissosteira* the ventral muscles of the first abdominal segment (fig. 35, *IS*) are attached anteriorly on a weakly developed ridge (*Ac*) which crosses the first abdominal sternum between the angles of the sternellar lobes of the metasternum. The line of this ridge appears externally as a faint transverse suture (fig. 30 A, D, *acs*). The ridge (fig. 35, *Ac*), therefore, is the antecosta of the first abdominal sternum, and the representative of the spinae of the prothoracic and metathoracic sterna. The median plate dovetailed into the metasternum (figs. 30 A, D, 35, *Pc*) is the enlarged precosta of the first abdominal sternum. It corresponds exactly with the postnotal plate of the metathorax (fig. 25, *PN3*), which is an extension of the precosta of the first abdominal tergum.



## III. THE THORACIC MUSCLES OF DISSOSTEIRA

The evolution of insect structure has been largely an evolution of mechanisms made up of the cuticula and the muscles. Though the study of the insect skeleton will remain the most important branch of insect anatomy for purposes of taxonomic description, it is becoming evident that the morphology of the skeleton is not to be understood without a knowledge of the relations that exist between the cuticular modifications and the muscles. Systematists and anatomists have consumed much time and have occupied much printed space with discussions of homologies between sclerites, which, in many cases, are of little value because the fundamental structure of the parts in question has not been studied and because mechanical relationships have been entirely ignored. The time is at hand when we must understand insects as living creatures rather than as museum specimens. Morphology must become a basis for the study of function, including both the physiological processes by which the insect is maintained as a living thing, and the mechanisms by which it directs its bodily activities.

A grasshopper furnishes a particularly good subject for the study of insect musculature. Not only are the individual muscles easily distinguished in dissections, but the muscles present are principally those that are common to all generalized insects. Fresh specimens do not serve well for the purpose of muscle study, but after twenty-four hours' immersion in 80 per cent alcohol the fiber bundles become more compact and are more readily seen as separate muscles. Since most of the insect's muscles are arranged laterally, a median sagittal section of the body will give the best approach to the muscles for an initial examination; but eventually it will be necessary to cut specimens into numerous pieces, for each muscle must be followed from one attachment to the other. Never accept a supposed observation for a fact until it is seen alike in at least two preparations—not that specimens differ, but that observations frequently do.

It is customary in describing muscles to follow them from their origins (fixed ends) to their insertions (movable ends), but the muscles of insects are in general more easily *studied* by finding the insertion points first and then tracing the bundles of fibers out to their basal attachments. The origins of muscles are likely to vary more in different segments and in different species than are the insertions, and branched muscles are often confusing until their common parts or apodemes of insertion are determined.

The student will find that the principal thoracic muscles of *Dissosteira* more nearly correspond with the description of the muscles of the field cricket, *Liogryllus* (*Acheta*) *campestris*, given by Carpen-

tier (1923) than with the description of the muscles of *Gryllus domesticus* given by Voss (1905). The musculature of the cricket is in some respects more elaborate than that of the locust; but the extra fibers constitute small and apparently secondary muscles that are not definitely repeated in insects generally. The account of the musculature of *Gryllus pennsylvanicus* given by DuPorte (1920) contains inaccuracies, especially with regard to the muscles of the legs; the leg muscles of *Gryllus* are in no essential way different from those of *Dissosteira*.

No attempt will be made in this paper to homologize the muscles of *Dissosteira* with those of other insects, or to correlate them with the muscles described by other writers, since this would add too much to the size of the paper. The student, however, should consult the recent descriptions of the thoracic musculature of insects contained in the works of Bauer (1910, 1924, adult *Dytiscus*), Speyer (1922, 1924, larval *Dytiscus*), Carpentier (1923, *Acheta campestris* and *Tachycinus asynamorus*), Weber (1927, *Tenthredinidae*; 1924, 1928, Lepidoptera; 1928a, *Aphis fabae*; 1929, *Psylla mali*), and Morison (1927, *Apis mellifera*). Berlese's (1909) review of the musculature of insects will need some revision in the light of more extensive comparative studies of insect muscles; but a general myology of insects can not yet be undertaken since we need more extensive information concerning such groups as Apterygota, Plecoptera, and Neuroptera.

The terminology of insect musculature offers some difficulty for the reasons that in different species the number of muscles in a functional group is variable, the attachments may shift from one point to another, and the functions of muscles undoubtedly homologous are often changed as a consequence of altered relations in the skeletal parts. In the following description of the thoracic musculature of the grasshopper individual muscles are designated numerically for convenience of reference only, and the series of numbers (46 to 139) follows the enumeration of the head muscles of *Dissosteira* given in a former paper by the writer (1928).

Dissection of the thoracic muscles is simplified when the general plan of the segmental musculature is understood. The thoracic muscles of insects fall into a few major groups which, in a general way, are as follows: (1) dorsal body muscles; (2) ventral body muscles; (3) tergo-sternal muscles; (4) special wing muscles; (5) pleuro-sternal muscles; (6) coxal wing muscles; (7) body leg muscles; (8) muscles of the leg segments; (9) muscles of the spiracles. In addition there are the muscles of the neck plates, and often oblique, lateral intersegmental muscles.

## MUSCLES OF THE NECK AND PROTHORAX

The prothoracic and neck muscles of the grasshopper are best studied from the mesal plane of the body. They may be exposed by cutting into lateral halves a specimen that includes the back of the head, the prothorax, and the mesothorax. Before removing the alimentary canal, a branched muscle should be observed going from the side of the protergum to the crop and the gastric caeca, which is,

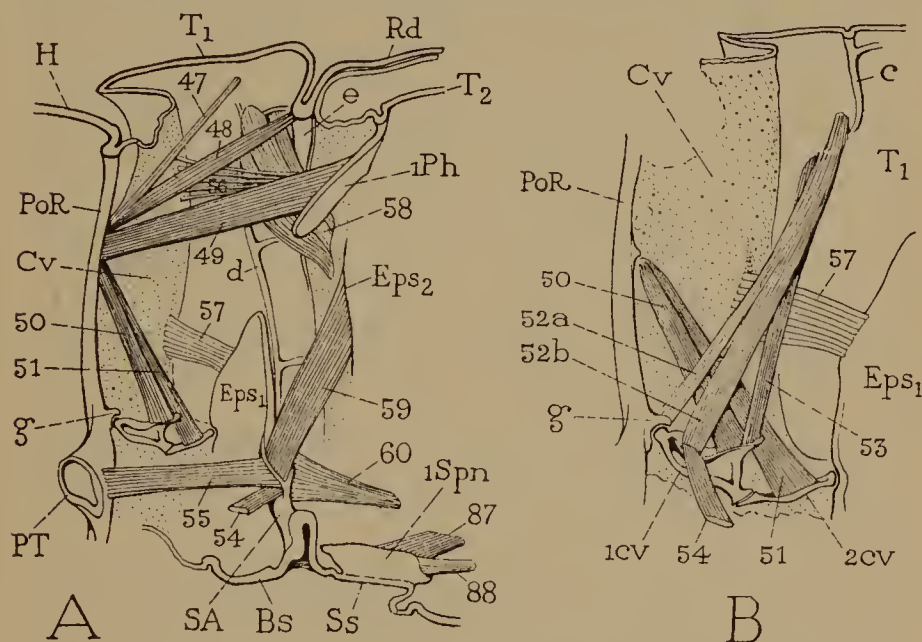


FIG. 32.—Muscles of the neck of *Dissosteira*, right side, internal view.

A, muscles extending between head and prothorax, omitting 52, 53, and 54, shown in B, inserted on first cervical sclerite. B, muscles of cervical sclerites.

Bs, basisternum of prothorax; c, first ridge of protergum; Cv, neck; 1cv, first cervical sclerite; 2cv, second cervical sclerite; d, second ridge of protergum; e, third ridge of protergum; Eps<sub>1</sub>, prothoracic episternum; Eps<sub>2</sub>, mesothoracic episternum; g, process of head articulating with first cervical sclerite; H, head; iPh, first phragma; PoR, postoccipital ridge of head; PT, base of posterior tentorial arm; Rd, posterior fold of protergum; SA, prosternal apophysis; 1Spn, first spina; Ss, spinasternum; T<sub>1</sub>, protergum.

46. *Posterior protractor of the crop and gastric caeca* (fig. 33 A).—A slender, branched muscle arising on lateral surface of protergum from lower end of first tergal ridge (c) just before base of tergal promotor of coxa (62); branching posteriorly to lateral wall of crop and tips of gastric caeca.

The alimentary canal and fat tissue should now be removed in order to expose the muscles in the side of the neck and prothorax, some of which extend from the mesothorax to the head. Functionally there are three groups of these muscles, namely, those that move the head, those that move the prothorax, and those that move the fore leg.



It is impossible to determine, from an anatomical study alone, the individual action of the muscles attached on the back of the head and on the cervical sclerites (fig. 32 A, B), since their functions may vary according to whether opposed sets of them act together or as antagonists. It is evident that the dorsal muscles (fig. 32 A, 47, 48, 49) and the ventral muscles (55) may tilt the head up or down respectively by pulling on opposite sides of the fulcrum of the cervical sclerites (*g*), or also that they may turn the head laterally if both sets on either side act as antagonists to those of the other side, while, finally, if they all act together they would become retractors of the head. The dorsal muscles of the cervical sclerites (A, B, 50, 51, 52, 53) must be the protractors of the head, since their combined pull would straighten the angles between the two sclerites of each pair and thus push the head forward. The oblique ventral muscles of the cervical sclerites (fig. 35, 54) would appear to be accessory to the lateral movement of the head.

47. *First protergal muscle of the head* (fig. 32 A).—A slender muscle arising dorsally on protergum; inserted dorso-laterally on postoccipital ridge of head (*PoR*).

48. *Second protergal muscle of the head* (fig. 32 A).—A larger muscle arising dorsally on third ridge (*e*) of protergum; inserted with 47 on postoccipital ridge of head.

49. *Longitudinal dorsal muscle of the neck and prothorax* (fig. 32 A).—A broad muscle from first thoracic phragma (*1Ph*) to postoccipital ridge of head just below 48.

50, 51. *Cephalic muscles of the cervical sclerites* (fig. 32 A, B).—Origins on postoccipital ridge below 49; both extend ventrally and posteriorly, the first (50) inserted on first cervical plate, the second (51) on second cervical plate.

52, 53. *Protergal muscles of the cervical sclerites* (fig. 32 B).—Origins dorso-laterally on protergum at lower end of first tergal ridge (*c*); both extend ventrally and anteriorly, crossing internal to 50 and 51, to insertions on first cervical sclerite, the first muscle with a branch (52a) to articular process (*g*) of head.

54. *Prosternal muscle of the first cervical sclerite* (figs. 32 A, B, 33 C, 35).—A horizontal, diagonal muscle arising on prosternal apophysis (figs. 32, 35); inserted anteriorly on first cervical sclerite of opposite side (figs. 32 B, 35), the right and left muscles crossing each other medially (fig. 35).

55. *First ventral longitudinal muscle* (figs. 32 A, 33 A, 35).—A broad, flat muscle from base of posterior arm of tentorium to apophysis of prosternum (figs. 32 A, 35, 54).



56. *Dorsal lateral neck muscle* (fig. 32 A).—A band of slender fibers from first phragma (*1Ph*) inserted on base of neck membrane (*Cv*).

57. *Ventral lateral neck muscle* (fig. 32 A, B).—A short, flat muscle from anterior edge of prothoracic episternum (*Eps<sub>1</sub>*), inserted on base of neck membrane (*Cv*).

The prothorax is movable on the mesothorax by two oblique, lateral intersegmental muscles on each side (fig. 32 A, 58, 59), and by three pairs of ventral intersegmental muscles (figs. 32 A, 35, 60, 87, 88).

58. *Tergo-pleural intersegmental muscle* (fig. 32 A).—A broad muscle of several sections, attached anteriorly on protergum behind upper end of ridge *d*; extends posteriorly and ventrally to intersegmental membrane just before upper end of mesepisternum (*Eps<sub>2</sub>*).

59. *Sterno-pleural intersegmental muscle* (figs. 32 A, 33 A, 35).—Attached anteriorly on upper end of prosternal apophysis (figs. 32 A, 33 A, *SA*); extends posteriorly and dorsally to dorsal end of anterior margin of mesepisternum (*Eps<sub>2</sub>*). In some insects this muscle is attached posteriorly on the anterior angle of the mesotergum.

60. *Second ventral longitudinal muscle* (figs. 32 A, 33 A, 35).—Extends between prosternal and mesosternal apophyses. Attached anteriorly by broad base on prosternal apophysis; tapers posteriorly to attachment on anterior margin of mesosternal apophysis (fig. 35).

The other two sternal muscles that move the prothorax are the third and fourth ventral longitudinals (figs. 32 A, 35, 87, 88) attached anteriorly on the first spina (*1Spn*), but they will be described with the mesothoracic muscles.

61. *Sterno-spinal muscle* (figs. 33 C, 35).—A very small muscle arising on base of prosternal apophysis (*SA*); the two from opposite sides converging posteriorly to insertions on anterior end of first spina (*1Spn*). Since the spinasternum (*Ss*) is but little movable on the prosternum (*S<sub>1</sub>*) in the grasshopper, this pair of muscles can act only as tensors or levators of the spinasternum.

The muscles that move the prothoracic leg of *Dissosteira* represent the *tergal promotor* (fig. 11, *I*), the *tergal remotor* (*J*), and the *sternal remotor* (*L*) of the primitive limb base, and the *abductors* (*M*) and the *adductors* (*N*) of the coxa. A representative of the *sternal promotor* (*K*) is absent in the prothorax of *Dissosteira*. The sternal remotors function as posterior rotators of the coxa by reason of the single articulation of the latter with the pleuron only; in *Dissosteira* one branch of the sternal remotor arises on the spina.

62. *Tergal promotor of the coxa* (fig. 33 A).—The largest muscle of the prothorax. Origin on upper lateral wall of protergum, posterior to lower end of first ridge (*c*); insertion ventrally on the small trochantin (fig. 33 A, B, D, *Tn*).

63. *First tergal remotor of the coxa* (fig. 33 A).—Origin on lateral wall of protergum mesad of upper end of 62 below ridge *f*; extends ventrally and posteriorly external to 59 and 60 to insertion on posterior angle of base of coxa (fig. 33 B, C, D).

64. *Second tergal remotor of the coxa* (fig. 33 A, B, C, D).—A short muscle arising on lateral wall of protergum (D) beneath ridge *i*; insertion on posterior angle of coxa (C, D).

65. *Third tergal remotor of the coxa* (fig. 33 A, B, C, D).—A slender muscle arising on protergum (D) in angle between ridges *e* and *h*; insertion ventrally on posterior angle of coxa.

66. *First posterior rotator of the coxa* (figs. 33 C, D, 35).—Origin on base of sternal apophysis (figs. 33 C, 35, *SA*); insertion on posterior angle of coxa.

67. *Second posterior rotator of the coxa* (figs. 33 C, D, 35).—Origin on side of spina (figs. 33 C, 35, *ISpn*); insertion on posterior angle of coxa.

68. *Abductor of the coxa* (fig. 33, B, D).—A flat, two-branched muscle arising on inner face of episternum (*Eps*), the larger branch (68*b*) dorsally, the smaller branch (68*a*) in anterior ventral angle; both inserted by a common stalk on outer rim of coxa (D) just before pleural coxal articulation (*CxP*).

69. *Adductor of the coxa* (fig. 33 C).—Origin on outer end of sternal apophysis (*SA*), or at union of the latter with pleural apophysis (*PLA*); insertion on inner rim of base of coxa (*Cx*).

The following nine muscles (70 to 78) pertain to the segments of the telopodite of the prothoracic leg. Three branches of the depressor of the trochanter (71) have their origins within the body.

70. *Levator of the trochanter* (fig. 36 A).—Origin dorsally in anterior part of coxa; fibers converge to insertion on tendon arising from dorsal lip of base of trochanter. This is the lifting muscle of the telopodite.

71. *Depressor of the trochanter* (figs. 33 A, B, C, 36 A).—A five-branched muscle, two groups of fibers arising in the coxa and three in the prothorax, all converging upon a strong apodeme arising from ventral lip of base of trochanter (fig. 36 A, 71*Ap*). The coxal branches arise anteriorly (71*a*) and posteriorly in ventral part of coxa; of the three body branches the first (71*b*) arises dorsally on anterior margin

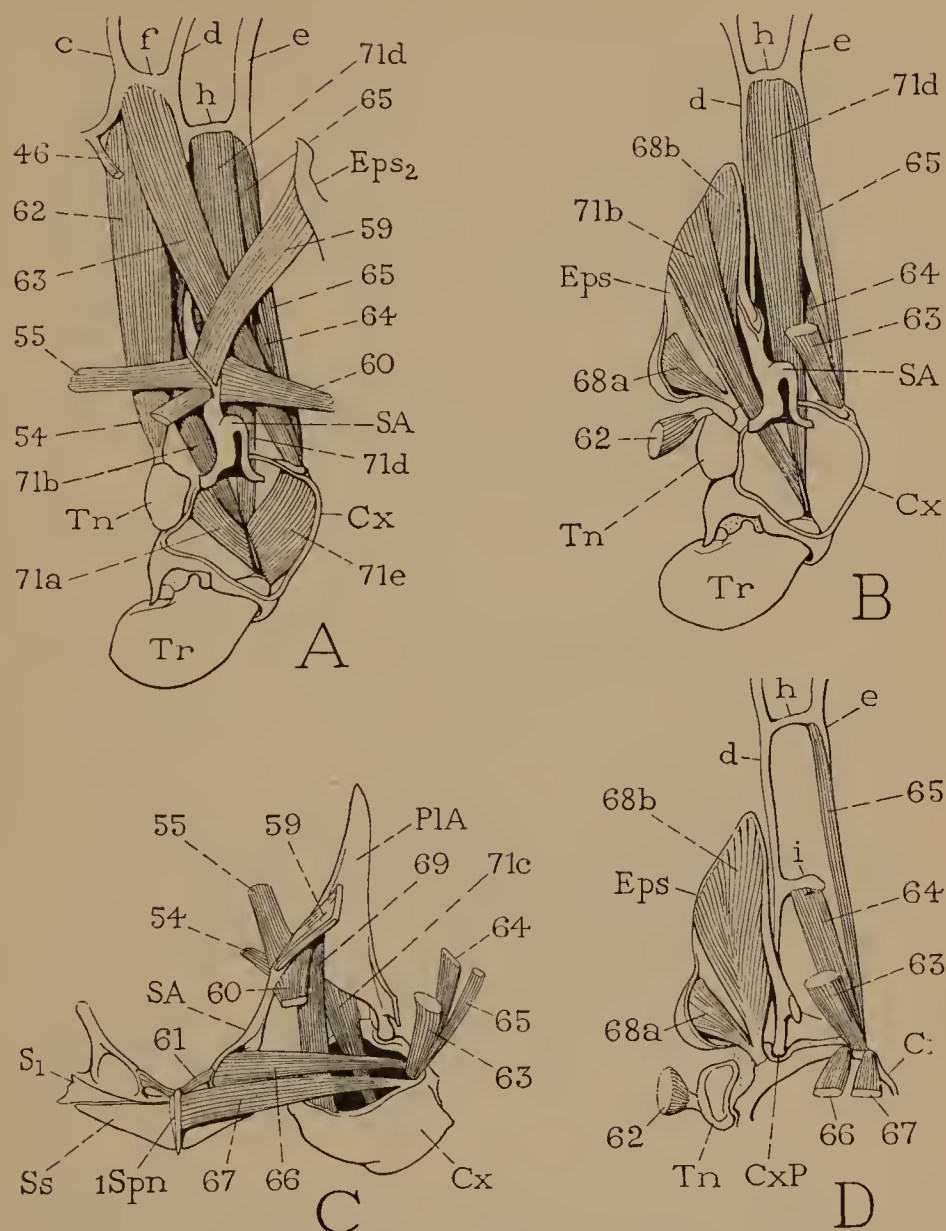


FIG. 33.—Musculature of the base of the fore leg of *Dissosteira*.

A, inner view of base of right leg, showing coxal and trochanteral muscles arising on lateral walls of protergum; tergal ridges lettered as on figure 20 B.

B, same as A but with inner muscles removed, showing coxal and trochanteral muscles arising on episternum, and posterior group on tergum.

C, posterior view of prosternum, right pleuron, and right coxa, showing leg muscles arising on sternum and pleural arm.

D, articular region of base of right coxa, and associated muscles, inner view.

of episternum (fig. 33 B, *Eps*), the second (71c) on ventral edge of pleural arm (fig. 33 C, *PlA*), the third (71d) on lateral wall of protergum (fig. 33 A, B) just below ridge *h*. These groups of fibers constitute the most powerful muscle of the leg and function as the depressor of the telopodite as a whole.

72. *Reductor of the femur* (fig. 36 A).—A short, broad muscle in posterior part of trochanter (*Tr*) arising on ventral wall of the segment; fibers extending dorsally and posteriorly to posterior rim of base of femur, giving the latter a slight posterior flexion.

73. *Anterior levator of the tibia* (fig. 36 A).—An extremely slender muscle arising anteriorly in base of femur; inserted by long, thread-like apodeme on a process from anterior side of base of tibia (as in middle leg, fig. 36 B, 105*Ap*).

74. *Posterior levator of the tibia* (fig. 36 A).—Origin dorsally in proximal part of femur; insertion by a strong tendon on posterior dorsal angle of base of tibia (as in middle leg, fig. 36 E, 106).

75. *Depressor of the tibia* (fig. 36 A).—Origin anteriorly (75a) and posteriorly on ventral wall of femur, with branch (75c) from base of trochanter (*Tr*); inserted by a strong tendinous apodeme arising from small ventral plate in membrane of femoro-tibial joint.

76. *Levator of the tarsus*.—Origin on distal third of dorsal wall of tibia; insertion on dorsal lip of base of tarsus.

77. *Depressor of tarsus*.—Origin on ventral wall of tibia; insertion on ventral lip of base of tarsus.

78. *Depressor of the pretarsus: retractor of the claws* (fig. 36 A).—This muscle comprises three branches, the principal one arising posteriorly in base of femur (fig. 36 A, 78), the other two in upper part of tibia; all inserted on a long tendon extending from femur through tibia and tarsus to unguitractor plate at base of claws.

The following two muscles are those of the first spiracle, but since the first spiracle is situated within the region of the prothorax, its muscles are to be classed as prothoracic. The mechanism of the spiracles will be discussed in Section VI.

79. *Closing muscle of the first spiracle* (fig. 51 B).—Origin on ventral process of peritreme (*l*); insertion on lever of posterior lip of spiracle (*i*).

80. *Opening muscle of the first spiracle* (fig. 51 B).—Origin on ventral process of peritreme; insertion on base of posterior lip of spiracle.



## MUSCLES OF THE PTEROTHORAX

The musculature of the wing-bearing segments differs in many respects from that of the prothorax, particularly in the great development of the dorsal longitudinal muscles (fig. 34, 81, 112), in the presence of large tergo-sternal muscles (83, 84, 113) and special wing muscles which are lacking in the prothorax, and in the presence of two pleuro-coxal muscles that become wing muscles in the adult.

The dorsal longitudinals and the tergo-sternals constitute a group known as the *indirect wing muscles* because they effect movements of

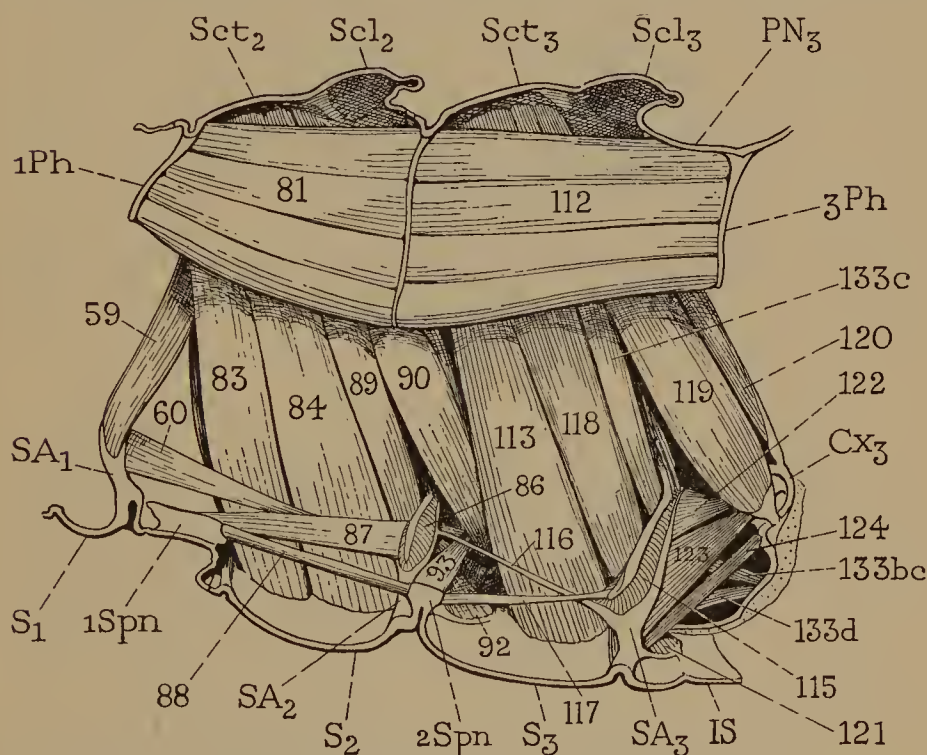


FIG. 34.—General view of the musculature in the right half of the pterothorax of *Dissosteira*. Median section, seen from the left.

the wings by alternate changes in the curvature of the tergum. There is but one special wing muscle in *Dissosteira* connected with each wing: this is the wing flexor (figs. 37 A, 85; 49, D), a short muscle having its origin on the pleuron and its insertion on the third axillary sclerite of the wing base. In many insects there are several small muscles from the upper parts of the pleuron to the edge of the tergum or to the base of the wing, but representatives of these muscles are absent in the grasshopper. The two pleuro-coxal muscles that become important wing muscles in the adult are apparently abductors of the coxa in the nymph (fig. 27 C, M', M''). The first is the pronator-

extensor of the wing (fig. 49,  $M'$ ), having its dorsal insertion on the basalar plates of the adult; the second is the depressor-extensor ( $M''$ ) with its insertions on the subalar plate. Associated with the first is a large muscle ( $E$ ) arising ventrally on the sternum. These three epipleural muscles ( $E$ ,  $M'$ ,  $M''$ ) together with the wing flexor ( $D$ ) constitute the so-called *direct wing muscles*, though only the flexor is a true wing muscle.

The ventral muscles of the pterothorax are small; those of the mesothorax (figs. 34, 35, 60, 87, 88) serve to move the prothorax; those of the metathorax (116, 117) can have but little motor function, since the mesothorax and metathorax are immovable on each other, and they are reduced mostly to tendinous strands. The muscles of the middle and hind legs are essentially the same as those of the prothoracic leg, but the muscles of the hind tibia are particularly large and not of the same relative size as those of the fore and middle legs.

A first dissection of the pterothoracic musculature should be made from the median plane of the body in a specimen cut into lateral halves (fig. 34) from which the alimentary canal and other visceral tissues have been removed.

#### THE MESOTHORACIC MUSCLES

81. *Longitudinal dorsal muscles* (fig. 34).—A large mass of fibers in each side of upper median part of mesothorax, attached anteriorly on lobes of first phragma ( $1Ph$ ) and posteriorly on middle phragma.

82. *Oblique dorsal muscles* (not shown in figures).—A small muscle laterad of longitudinal dorsals; arising on lateral part of scutum, extending posteriorly and ventrally to insertion on outer part of middle phragma.

83. *First tergo-sternal muscle* (fig. 34).—Attached dorsally on posterior part of lateral prescutal lobe; attached ventrally on anterior part of mesosternum.

84. *Second tergo-sternal muscle* (fig. 34).—A very large muscle immediately posterior to 83; attached dorsally by inner branch on middle of lateral scutal area, and by outer branch on marginal lobe of scutum behind posterior articulation of first axillary; attached ventrally on mesosternum before inner margin of coxal cavity.

85. *Pleuro-alar muscle: flexor of the wing* (fig. 37 A).—This muscle lies laterad of the series of dorsoventral muscles in the side of the segment and may be noted after the latter are removed. It arises by a broad base on upper part of pleural ridge ( $PIR$ ), and goes dorsally and posteriorly between 98 and 99 into wing base where it is inserted on the third axillary (fig. 49, 3A $x$ ).

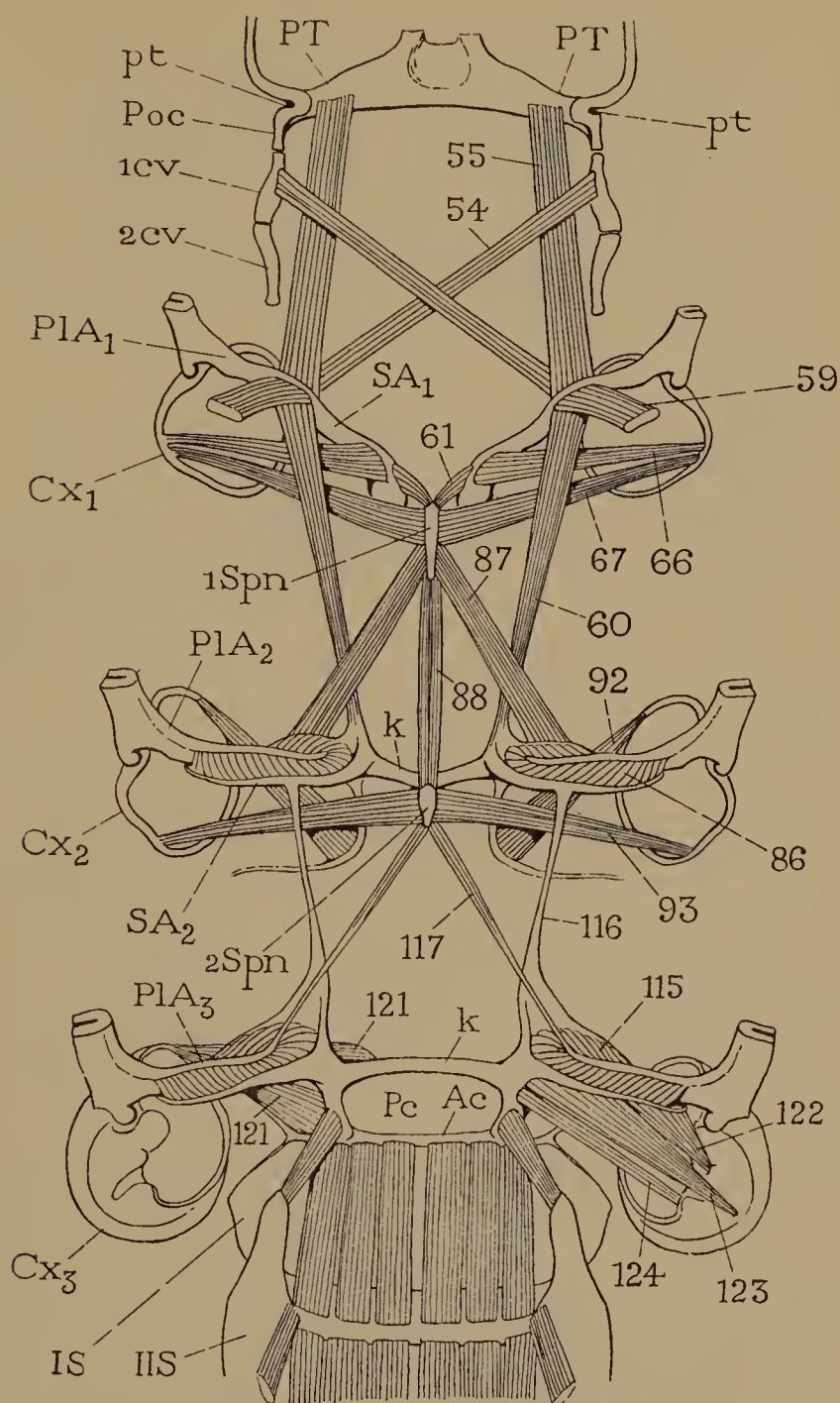


FIG. 35.—General view of the ventral musculature of *Dissosteira* from the head to the second abdominal segment.

86. *Pleuro-sternal muscle* (figs. 34, 35).—A dense mass of very short fibers connecting the approximated ends of the pleural apophysis and the sternal apophysis.

87. *Third ventral longitudinal muscle* (figs. 34, 35).—Attached laterally on first spina (*1Spn*) ; extends posteriorly and laterally over posterior end of 60 to anterior edge of apophysis of mesosternum (*SA<sub>2</sub>*).

88. *Fourth ventral longitudinal muscle* (figs. 34, 35).—A slender muscle attached anteriorly on first spina (*1Spn*) and posteriorly on second spina (*2Spn*).

The following thirteen muscles (89-101) include the muscles of the base of the leg and the principal direct muscles of the wing.

89. *Tergal promotor of the coxa* (fig. 34).—Lies close behind 84 in the innermost series of lateral muscles. Origin on scutum ; insertion on stalked disc (fig. 37 A, B, C, 89) arising from articular membrane at anterior angle of coxa close to lower end of trochantin (B, C, *Tn*). The representative of this muscle in the prothorax (fig. 33 A, 62) is inserted on the trochantin, as it is in most insects in which the trochantin is well developed.

90. *First tergal remotor of the coxa* (fig. 34).—Origin on scutum ; goes ventrally posterior to pleural arm to insertion on stalked disc arising from inner posterior angle of coxa (fig. 37 A, B, 90).

91. *Second tergal remotor of the coxa* (fig. 37 A).—A slender muscle arising on scutum from outer end of ridge *s* (fig. 22 B) ; goes obliquely ventrally and posteriorly to slender apodeme arising from extreme posterior angle of coxa (fig. 37 A, B, 91). This muscle is the last of the tergal muscles of the mesothorax ; it lies just external to posterior border of 90 and is partially visible from median plane (fig. 34) between 90 and 113.

The group of mesothoracic muscles attached dorsally on the tergum includes two segmental branches of the depressor of the trochanter (103) which will be described later. When the tergal muscles have been removed there is exposed a second or outer set of lateral muscles having their origin on the pleuron (fig. 37 A). These muscles include the abductors of the coxa, and the direct muscles of the wing. The wing flexor (85) of the latter group has already been described as a pleuro-alar muscle ; the others are pleuro-coxal, with one pleuro-sternal muscle. Ventrally there will be seen also the sterno-coxal muscles, or rotators of the coxa, a description of which will logically follow that of the tergo-coxal muscles.



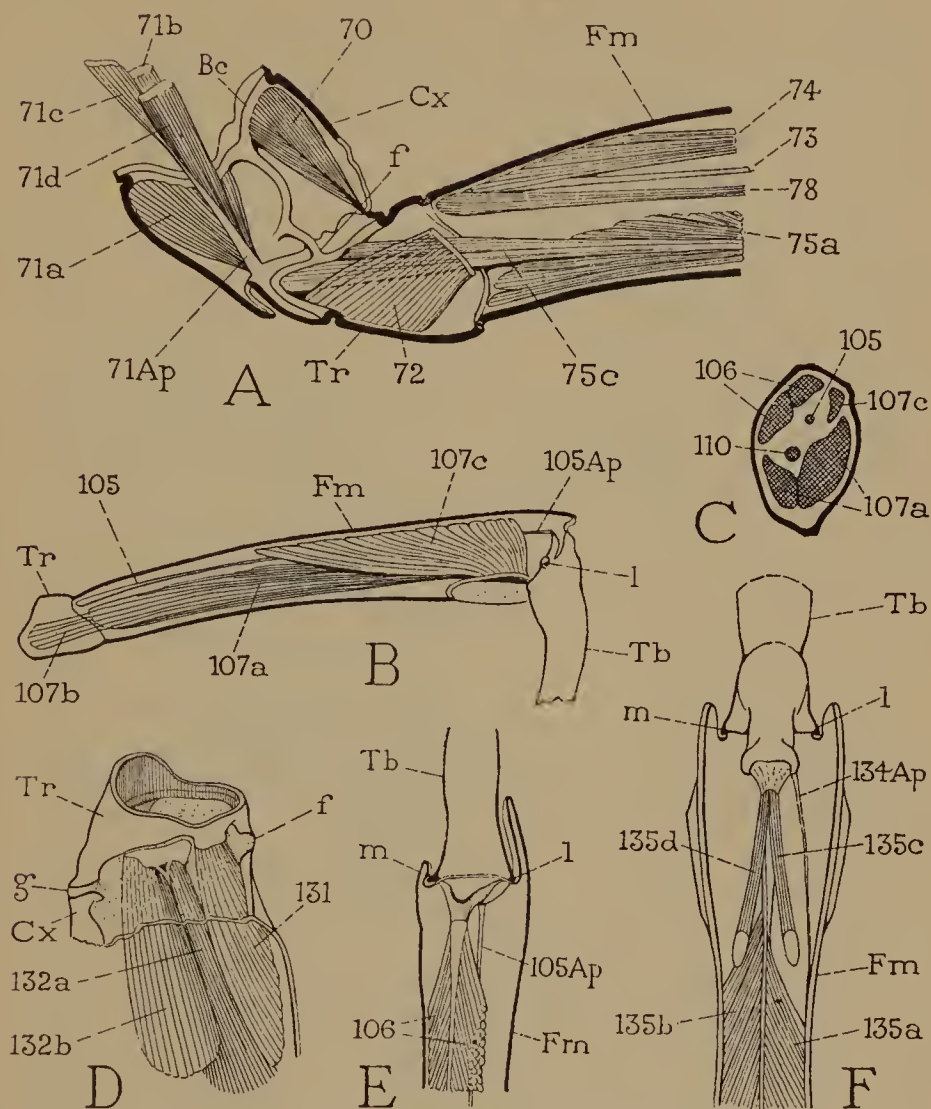


FIG. 36.—Leg musculature of *Dissosteira*.

A, posterior view of muscles in proximal part of right fore leg, including coxa (*Cx*), trochanter (*Tr*), and base of femur (*Fm*).

B, anterior and ventral muscles of tibia arising in femur and trochanter of left middle leg.

C, cross-section near middle of second left tibia, proximal surface of distal half, showing positions of tibial muscles.

D, dorsal view of trochanter (*Tr*) of left hind leg, showing anterior and posterior coxo-trochanteral articulations (*f*, *g*), and levator muscles of trochanter arising in coxa.

E, dorsal view of femoro-tibial joint of left middle leg, showing anterior and posterior articulations (*l, m*), and bases of levator muscles of tibia.

F, corresponding view of femoro-tibial joint of left hind leg.

92. *Anterior rotator of the coxa* (figs. 34, 35, 37).—Origin on sternellar lobe of mesosternum (figs. 34, 35); extends anteriorly and outward to anterior angle of coxa (figs. 35, 37 A, B, C).

93. *Posterior rotator of the coxa* (figs. 34, 35, 37).—Origin on second spina (figs. 34, 35); extends outward, above 92, to posterior inner angle of coxa (figs. 35, 37 A, B).

94, 95. *First and second abductors of the coxa* (fig. 37 A).—Origin on anterior ventral area of episternum (*Eps*); fibers of each converge to a pair of long, flat apodemes arising anteriorly on outer margin of coxa (fig. 37 B, C, 94, 95).

96. *Third abductor of the coxa* (fig. 37 A).—A wide, flat, fan-shaped muscle arising on episternal area posterior and dorsal to 95; fibers converging to insertion on a slender apodeme arising in articular membrane laterad of base of coxa just anterior to pleural articulation (fig. 37 B, 96).

97. *First pronator-extensor of the forewing* (fig. 37 A).—A large muscle inserted dorsally on first basalar plate (*IBa*); extending ventrally to attachment on lateral part of sternum before base of middle leg.

98. *Second pronator-extensor of the forewing* (fig. 37 A).—Insertion dorsally close to 97 on first basalar plate (*IBa*); attached ventrally on bases of apodemes of first and second abductors of coxa (fig. 37 B, C, 98).

99. *Depressor-extensor of the forewing* (fig. 37 A).—Inserted dorsally on subalar plate of wing base (*Sa*); attached ventrally on flat extension of basicoxal ridge (fig. 37 B, 99) in meral region of coxa (*Mer*) posterior to pleural articulation (*c*).

100. *First adductor of the coxa* (fig. 37 A).—A broad flat muscle arising on posterior margin of mesosternal apophysis; insertion on inner rim of coxa (A, B, 100).

101. *Second adductor of the coxa* (fig. 37 A).—A smaller muscle arising on mesosternal apophysis; inserted on posterior angle of coxa (A, B, 101) between attachments of 90 and 91.

The telopodite of the middle leg, or that part of the limb beyond the coxa, has the same musculature as the telopodite of the first leg; its muscles are the following:

102. *Levator of the trochanter*.—Origin dorsally in base of coxa; insertion on dorsal lip of base of trochanter.

103. *Depressor of the trochanter*.—A five-branched muscle with all branches inserted on a tongue-like apodeme arising from ventral lip of base of trochanter. Two branches arise ventrally in the coxa, one

anteriorly, the other posteriorly; the others take their origin in the mesothorax. The first and second body branches arise on scutum, one medially the other on lateral margin, both pass into coxa anterior to pleural arm; the third body branch arises on ventral margin of mesosternal apophysis. The trochantinal muscles effect the movement of the telopodite as a whole.

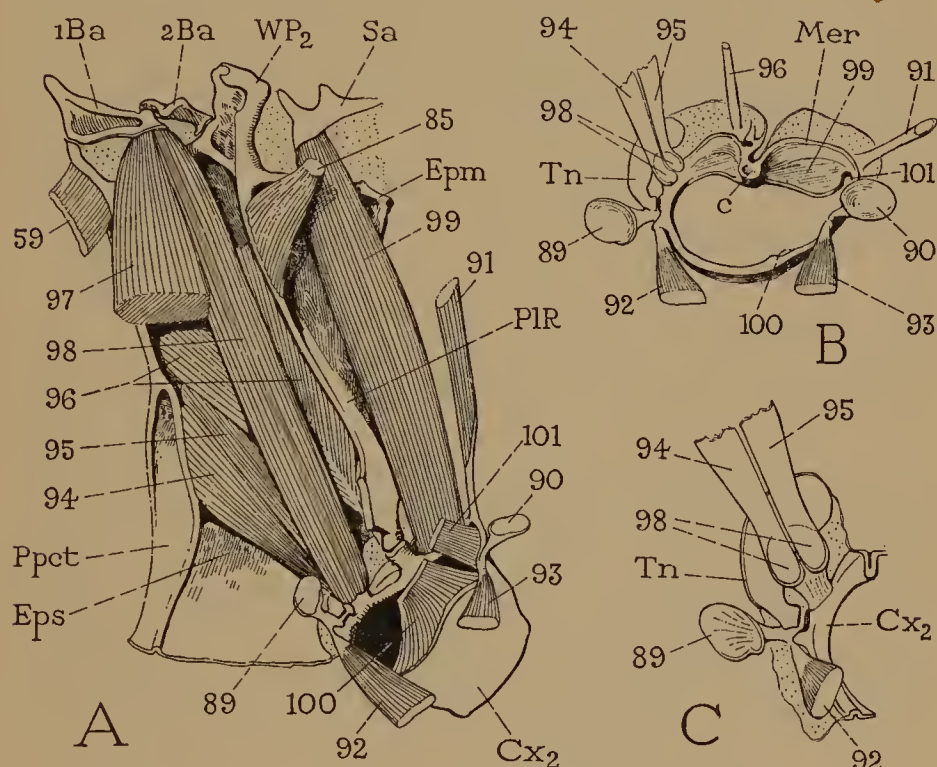


FIG. 37.—Coxal musculature of the middle leg of *Dissosteira*.

A, general view of pleural muscles, right side, inner view, and bases of sternal coxal muscles.

B, base of coxa, inner view, showing muscle attachments.

C, anterior rim of coxa ( $Cx$ ), trochantin ( $Tn$ ), and attachments of associated muscles, inner view.

104. *Reductor of the femur*.—A sheet of very delicate fibers in posterior part of trochanter, arising in base of latter, inserted on posterior rim of base of femur. This muscle is much weaker than the corresponding muscle of the prothoracic leg (fig. 36 A, 72), the femur of the middle leg being scarcely movable on the trochanter.

105. *Anterior levator of the tibia* (fig. 36 B, C).—A delicate, attenuate muscle arising anteriorly in base of femur; inserted by a long tendon-like apodeme arising from dorsal end of a slender process from anterior margin of base of tibia (fig. 36 E, 105Ap).

106. *Posterior levator of the tibia* (fig. 37 C, E).—A long, pinnate muscle with fibers arising on almost entire length of dorso-posterior wall of femur; inserted by strap-like tendon on dorsal angle of base of tibia (E, 106).

107. *Depressor of the tibia* (fig. 36 B, C).—The largest muscle in the middle femur, comprising three groups of fibers, all inserted on a long apodeme arising from small plate in ventral membrane of knee joint. Principal group of fibers (B, 107a) forms a long pinnate muscle arising ventrally in proximal part of femur; second group a small bundle of fibers (107b) arising in base of trochanter and joining with those of first group; fibers of third group (107c) arise anteriorly and dorsally in distal two-thirds of femur and converge ventrally to insertion on base of depressor apodeme.

108. *Levator of the tarsus* (fig. 42 A).—Origin dorsally in distal third of tibia; insertion on dorsal lip of base of tarsus.

109. *Depressor of the tarsus* (fig. 42 A).—Origin ventrally in distal three-fourths of tibia; insertion on ventral lip of base of tarsus.

110. *Depressor of the pretarsus: retractor of the claws* (figs. 36 C, 42 A, C).—Fibers arising in femur and tibia; inserted on long, thread-like apodeme arising from unguitractor plate at base of claws (fig. 42 C, 110Ap) and extending through tarsus (A) and tibia, and into femur. Principal group of fibers a long, tapering bundle (fig. 36 C, 110) arising proximally on posterior wall of femur and inserted on end of tendon; two smaller groups of fibers in upper end of tibia, one arising anteriorly in base of tibia, the other dorsally, both inserted on tendon just above middle of tibia.

Since the second thoracic spiracle lies within the region of the mesothorax, its muscle belongs to the same segment.

111. *Closing muscle of the second spiracle* (fig. 52 B).—Origin on small lobe (o) of posterior dorsal margin of mesocoxal cavity; insertion on ventral lobe of spiracular lips (n).

#### THE METATHORACIC MUSCLES

The musculature of the metathorax almost duplicates that of the mesothorax, with the principal difference that there are no oblique dorsal muscles and that there is only one pair of tergo-sternals in the metathorax.

112. *Longitudinal dorsal muscles* (fig. 34).—Most of the fibers extend between middle phragma and third phragma (3Ph), though a few dorsal ones are attached posteriorly on the postnotal plate (PN<sub>3</sub>).



113. *Tergo-sternal muscle* (fig. 34).—A large muscle, the first of the inner lateral series in metathorax, attached dorsally on lateral prescutal lobe, and below by a wide base on lateral part of sternum before coxal cavity. This muscle corresponds with 83 of the mesothorax, a scuto-sternal muscle (84) being absent in the metathorax.

114. *Pleuro-alar muscle: flexor of the hind wing* (fig. 38, 114).—This muscle consists of two bundles of fibers in metathorax, one external, the other internal, both arising from upper end of pleural ridge, and inserted on ventral surface of third axillary sclerite of wing base. The outer muscle is not visible from mesal plane until the first is removed.

115. *Pleuro-sternal muscle* (figs. 34, 35).—A dense mass of very short fibers connecting pleural apophysis with apophysis of metasternum.

116. *Fifth ventral longitudinal muscle* (figs. 34, 35).—A strong fiber, apparently a sclerotized muscle, extending from posterior edge of mesosternal apophysis ( $SA_2$ ) to median anterior angle of metasternal apophysis ( $SA_3$ ).

117. *Sixth ventral longitudinal muscle* (figs. 34, 35).—A slender muscle arising on second spina ( $2Spn$ ), becoming tendinous posteriorly; extends posteriorly and laterally to inner extremity of pleural apophysis of metathorax.

The ventral longitudinal muscles of the metathorax have evidently lost their contractile nature because of the fusion of the mesosternum and metasternum, and are converted mostly into sclerotic strands to brace the pull of the mesothoracic ventral muscles (62, 87, 88) on the sternal plates of the prothorax.

The following thirteen muscles (118 to 130) are muscles of the metacoxa and the hind wing.

118. *Tergal promotor of the coxa* (figs. 34, 38 A).—Lies immediately behind the tergo-sternal (fig. 34, 113). Arises dorsally on lateral area of scutum (fig. 38 A); inserted ventrally on apodemal disc of anterior angle of coxa (fig. 38 D, F, 118).

119. *First tergal remotor of the coxa* (figs. 34, 38 A).—A large muscle arising from posterior scutal margin; goes downward and posteriorly, behind pleural arm, to apodemal disc on posterior inner angle of coxa (fig. 38 D, F, 119).

120. *Second tergal remotor of the coxa* (figs. 34, 38 A).—A slender muscle lying close behind 119, tapering ventrally to slender apodeme arising from extreme posterior angle of coxa (fig. 38 B, D, F, 120).



The innermost series of lateral muscles includes two body branches of the trochanteral depressor (fig. 38 A, 133c) which will be described later. By removing the muscles attached on the tergum, there is exposed the outer series of pleural lateral muscles pertaining to the leg and wing, and the sternal muscles of the coxa.

121. *Anterior rotator of the coxa* (figs. 34, 35, 38 E).—A large muscle with fibers arising in two groups, one from lateral part of sternum before base of sternal apophysis, the other from sternellar lobe behind the apophysis; all fibers converge to insertions on anterior angle of coxa just mesad of stalked apodeme of 118 (fig. 38 D, F, 121).

122, 123, 124. *First, second, and third posterior rotators of the coxa* (figs. 34, 35, 38 E).—Origins on posterior margin of lateral arm of metasternal apophysis; insertions posteriorly on base of coxa, the first (fig. 38 D, E, F, 122) on process of meral region, the second (123) just within posterior angle of coxa, the third (124) on posterior part of meral rim of coxa.

The innermost pleural muscles are the large basalar and subalar wing muscles (fig. 38 B, 127, 128, 129); external to them are the abductors of the coxa.

125. *First abductor (accessory promotor) of the coxa* (fig. 38 C).—A small muscle arising from anterior edge of metepisternum just behind and below second spiracle (2Sp); insertion anteriorly on external margin of coxa (fig. 38 C, D). Anatomically this muscle evidently belongs to the abductor system of the coxa, but apparently it functions as an accessory of the tergal promotor (D, 118).

126. *Second abductor of the coxa* (fig. 38 C).—A large flat muscle arising on inner face of episternum and on anterior surface of pleural ridge; fibers converging to insertion on slender apodeme (fig. 38 D, F, 126) arising in articular membrane at base of coxa just before pleural articulation.

127. *First pronator-extensor of the hind wing* (fig. 38 B).—A large muscle attached dorsally on first basalar plate (1Ba), and ventrally on lateral part of sternum before coxa and laterad of base of the tergo-sternal muscle (figs. 34, 38 A, 113).

128. *Second pronator-extensor of the hind wing* (fig. 38 B).—Lies close behind 127; attached dorsally on second basalar plate (2Ba), ventrally on lateral rim of coxa (fig. 38, D, F, 128) anterior to pleural articulation (c).

129. *Depressor-extensor of the hind wing* (fig. 38 B).—A powerful muscle, attached dorsally on inner disc of subalar plate (Sa), and ventrally on wide basicostal surface of meral region of coxa (fig. 38 D, F, 129).



130. *Adductor of the coxa* (fig. 38 C, D, E, F).—Origin on posterior surface of lateral arm of sternal apophysis (E) beneath base of first posterior rotator (122); goes posteriorly and downward below 123 and 124 to posterior part of inner margin of coxa (C, D, E, 130).

The following muscles belong to the telopodite of the hind leg. The total number is the same as in the fore and middle leg, but there are two distinct levators of the trochanter, and a reductor of the femur is lacking.

131. *Anterior levator of the trochanter* (figs. 36 D, 39).—Origin on dorsal part of anterior wall of coxa; insertion on anterior lobe of dorsal rim of trochanter (fig. 36 D).

132. *Posterior levator of the trochanter* (figs. 36 D, 39).—A two-branched muscle arising dorsally in base of coxa; both branches (132a, 132b) inserted on levator apodeme and supporting plate in dorsal articular membrane close to rim of trochanter (fig. 36 D).

133. *Depressor of the trochanter* (figs. 38 A, E, 39).—This muscle, as in the other legs, consists of five branches, two of which arise in the coxa, and three in the metathorax; all are inserted on ventral rim of trochanter and together constitute a strong depressor of the telopodite. The coxal branches arise one anteriorly (fig. 39, 133a), the other posteriorly in ventral part of coxa. Two of the body branches arise on scutum of metatergum, one from lateral margin, the other (fig. 38 A, 133c) from center of lateral field. These two branches converge downward and unite before the pleural arm in a broad, tough band of fibers that curves posteriorly beneath the pleural arm (PLA) to enter the coxa. The third body branch arises from under surface of lateral arm of sternal apophysis (fig. 38 A, E, 133d).

134. *Anterior levator of the tibia* (figs. 36 F, 39).—This muscle appears to be represented in the hind leg of *Dissosteira* by only a very delicate tendinous strand arising from the anterior angle of the tibial base (134Ap), and extending proximally for a short distance against the anterior wall of the distal part of the femur. The writer was unable to discover muscle fibers attached to this tendon.

135. *Posterior levator of the tibia* (figs. 36 F, 39).—This great muscle occupies most of the cavity of the femur (fig. 39 A, B). The fibers arise in short, overlapping bundles from anterior and posterior walls of femur where they are attached on the spaces between the "fish-bone" ridges, with dorsal fibers of posterior set (135b) arising in dorsal crest of femur. Anterior and posterior fibers converge to sides of a large, thin, flat apodeme that tapers distally to a thick stalk



(fig. 39 A, *135Ap*) arising from dorsal margin of base of tibia. On the base of this apodeme are inserted two short, strap-like branches (fig. 36 F, *135c*, *135d*) arising dorsally in distal part of femur.

*136. Depressor of the tibia* (fig. 39).—A relatively small muscle with long, slender fibers (*136a*) arising in ventral part of femur and converging to sides of long, tapering apodeme arising in ventral membrane of knee joint. The terminal, strap-like part of this apodeme slides over a strong, internal process (*a*) of ventral wall of femur.

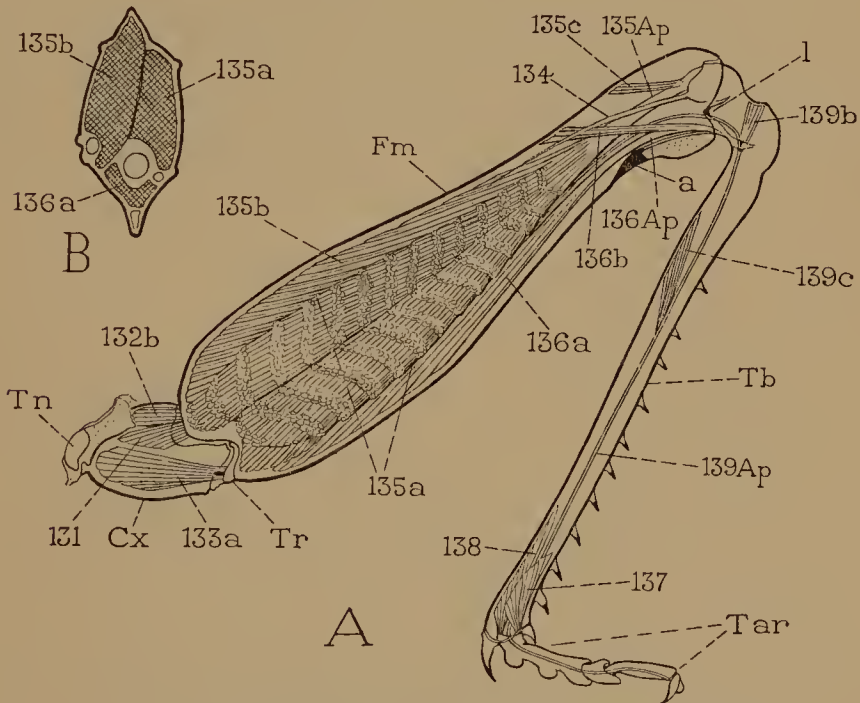


FIG. 39.—Musculature of the hind leg of *Dissosteira*.

A, left leg, anterior (outer) view. B, cross-section through basal half of left femur, proximal end of distal piece, showing positions of levator and depressor muscles of tibia and of principal tracheae.

Two small, anterior and posterior bands of fibers, arising on dorsal wall of femur, are inserted on apodeme near its base, the anterior one (*I36b*) shown in the figure.

137. *Levator of the tarsus* (fig. 39).—A very small dorsal muscle in distal end of tibia, inserted on dorsal rim of base of tarsus.

138. *Depressor of the tarsus* (fig. 39).—A small muscle, but longer than the levator, arising ventrally in distal part of tibia, inserted on ventral lip of base of tarsus.

139. *Depressor of the pretarsus: retractor of the claws* (fig. 39).—Comprises three small groups of fibers, one arising posteriorly in ventral part of femur among fibers of tibial depressor, the second (139*b*)

in proximal end of tibia, the third (139c) on ventral wall of basal half of tibia; all inserted on fine, tendon-like apodeme (139 Ap) arising from unguitractor plate at base of claws.

#### IV. THE LEGS AND THEIR MUSCLES

The legs of the grasshopper are all of typical form and segmentation, but the hind legs, being specially developed as organs of leaping, are not only of greater size than the others but differ from them in certain details of structure and in the relative proportions of some of the muscles. When the grasshopper sits in an ordinary resting position it supports itself principally on the first and second pairs of legs, the tibiae of the hind legs being flexed against the under surfaces of

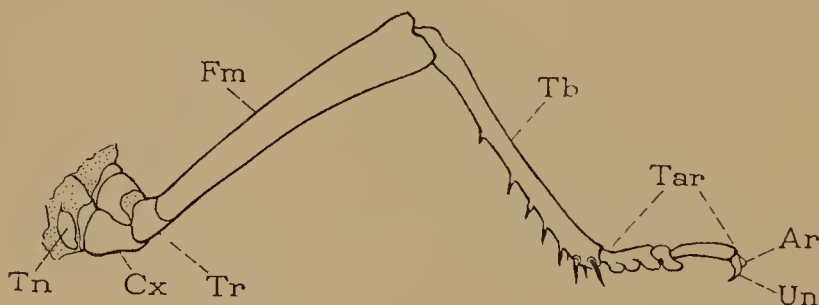


FIG. 40.—Middle leg of *Dissosteira*, anterior surface.

*Ar*, arolium; *Cx*, coxa; *Fm*, femur; *Tar*, tarsus; *Tb*, tibia; *Tn*, trochantin; *Tr*, trochanter; *Un*, claw.

the femora, with the knees usually held low and the tarsi barely touching the ground. (The grasshopper of illustrations commonly rests on all three pairs of legs, with the hind knees elevated and the tibiae extended.) In its natural resting attitude, the insect is always ready for a leap, the spring being caused by a forcible extension of the hind tibiae, probably accompanied by a strong depression of the trochantero-femoral parts of the legs. The chief function of the first and second legs is the support of the body and the directing of the few movements of walking or of changing the resting position; the first legs are actively used also during feeding for grasping and manipulating the edge of the leaf. When the grasshopper walks the hind legs are used with the others in the usual fashion.

In describing the legs it is customary to use terms of orientation as they would apply if the appendage were extended laterally at right angles to the body. Preaxial and postaxial surfaces are called *anterior* and *posterior*, and upper and lower surfaces are *dorsal* and *ventral*.

## STRUCTURE OF THE LEGS

The general form of a grasshopper's leg is shown in the illustration of the middle leg of *Dissosteira* (fig. 40). The appendage consists of a *coxa* (*Cx*), a *trochanter* (*Tr*), a *femur* (*Fm*), a *tibia* (*Tb*), a three-segmented *tarsus* (*Tar*), and a *pretarsus* comprising a pair of lateral claws (*Un*) and a median *arolium* (*Ar*). In the articular membrane before the base of each coxa there is a small trochantinal sclerite (*Tn*), best developed in the prothorax.

Each leg is set into a membranous area, or *coxal corium* (fig. 26), occupying an oval interruption in the sclerotic wall of the body between the pleuron and the sternum, known as the *coxal cavity*, the rim of which is reinforced by a submarginal inflection. The coxa is hinged to the body wall by only a single articulation, which is with the pleuron. The rudimentary trochantin (fig. 40, *Tn*) does not restrict the movement of the coxa. The anterior and middle coxae are free to move in any direction, but the hind coxae, which are directed posteriorly, have a more limited range of motion. The number of muscles inserted upon the hind coxae, however, suggests that what little movement these coxae possess is of much importance in the function of the hind legs.

It should be noted that the articulating surfaces of the pleuro-coxal hinge are formed by inflections of the body and coxal walls, and therefore lie on the *inner* surfaces of the latter (fig. 41 D). In this respect the basal joint of the leg differs from the basal articulations of the head appendages with the head wall, for the latter are external surfaces of contact lying outside the articular membranes. The peculiar character of the pleuro-coxal (subcoxo-coxal) articulations attests, therefore, that these articulations are not homologous with the basal articulations of the gnathal appendages on the edge of the epicranium.

The coxo-trochanteral joint and the articulations between the segments of the telopodite, except the trochantero-femoral joint, which is but little movable, are all of the dicondylic hinge type with anterior and posterior articulating points on a horizontal axis transverse to the length of the leg segments. Movement at these joints is approximately in the same vertical plane. The trochanters are closely attached to the femora, but the hinge lines lie in a vertical plane, and the presence of a posterior femoral muscle in the trochanter of the first and the second leg (fig. 36 A, 72) shows that the primitive motions at the trochantero-femoral joint were movements of production and reduction. The segments of the tarsus are movable on each other, but since they have no musculature, they can be moved only as they are influenced by the tendon of the unguis retractor which passes through them (fig. 44, *x*).

*The coxae.*—The three coxae of the grasshopper differ somewhat in their positions on the body. The first is the most freely movable; it projects downward and its base is almost horizontal. The second coxa is directed outward, downward, and posteriorly; its base lies in an oblique plane between the pleuron and the sternum. The hind coxa is directed posteriorly; its basal aperture is on the inner face and lies in an approximately vertical, longitudinal plane.

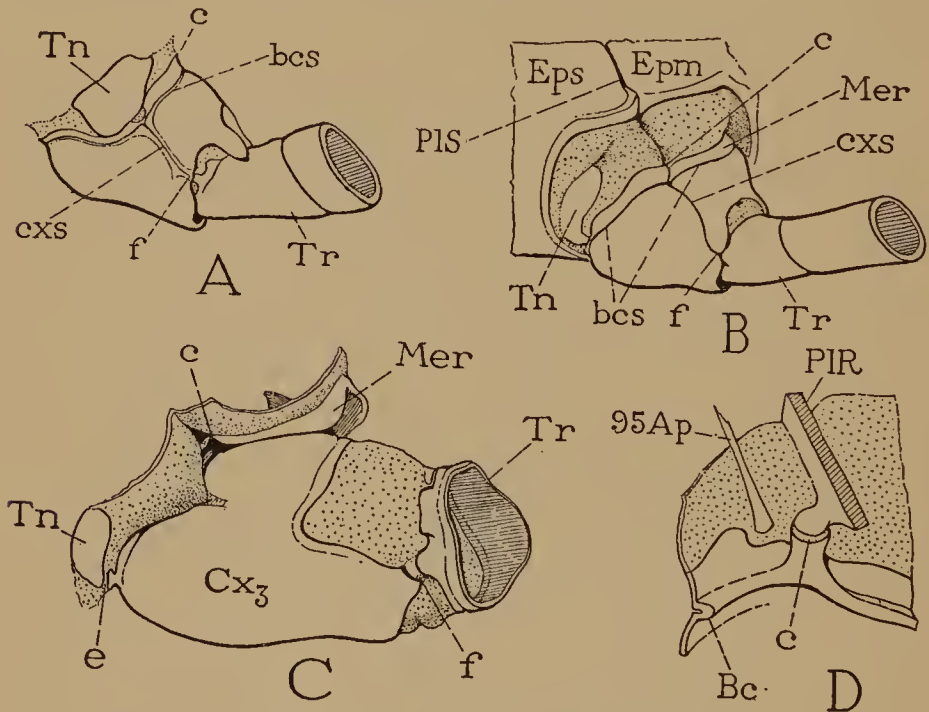


FIG. 41.—Structure of the coxae of *Dissosteira*.

A, first coxa and base of telopodite, left, anterior surface. B, base of middle leg, left, anterior surface. C, hind coxa and trochanter, left, anterior (outer) surface. D, articulation of middle coxa to pleural process, right, inner view.

95Ap, apodeme of second abductor of middle coxa; Bc, basicosta of coxa; bcs, basicostal suture; c, pleural articulation of coxa; Cx<sub>3</sub>, hind coxa; cxs, coxal suture; Epm, epimeron; Eps, episternum; f, anterior coxo-trochanteral articulation; Mer, meron; Pls, pleural suture; Tn, trochantin; Tr, trochanter.

Each coxa presents a well-marked basal rim, or *basicoxite*, set off by a submarginal *basicostal suture* (fig. 41 A, B, bcs) which forms internally a strong *basicosta* (D, Bc). Laterally the costa of the middle coxa (fig. 37 B) and of the hind coxa (fig. 38 D, F) are enlarged into wide, shelf-like plates for the accommodation of muscle attachments. The basicoxite is very narrow or obsolete on the mesal surface of the coxa, but on the lateral surface it forms a distinct prearticular and a postarticular lobe, the latter being known as the *meron* (fig. 41 B, Mer). The basicoxal lobes are well developed on the hind coxa (C)



but they are inconspicuous externally because each is bent outward and flattened upon the dorsal wall of the coxa. The articular surface (*c*) by which the coxa is hinged to the internal coxal process of the pleuron (*D*) is strongly inflected mesally in such a manner as to bring the point of suspension near the central axis of the coxa, thus giving the coxal muscles a leverage on all sides of it (fig. 43). Each coxa has a dicondylic hinge with the trochanter (fig. 36 D, *f, g*), the axis of which is horizontal and transverse to the length of the leg. The dorsal surface of the coxa is deeply emarginate between the hinge points, and the ample articular membrane that occupies the notch allows a free upward movement of the telopodite. When the latter is deflexed, the ventral lip of the trochanter passes inside the lower edge of the coxa.

The anterior wall of the prothoracic coxa is marked by a *coxal suture* (fig. 41 A, *cxs*) which extends from the anterior trochanteral articulation (*f*) to the basicostal suture at the articulation of the trochantin (*Tn*). The middle coxa (*B*) has a similar suture (*cxs*) ending at the trochanteral articulation (*f*), but it begins basally at the pleural articulation (*c*) and thus falls in line with the pleural suture (*PIS*) of the mesopleuron. The suture is absent in the hind coxa (*C*). The coxal suture, when present, forms a ridge on the inner surface of the coxal wall (fig. 36 A), the purpose of which is evidently to strengthen the latter.

A coxal structure such as that of the middle leg of the grasshopper (fig. 41 B), in which the anterior wall is divided by a groove (*cxs*) continuous with the pleural suture, is likely to be confused with the quite different structure illustrated by the coxa of *Panorpa* (fig. 14 A), in which the postarticular part of the basicostal suture (*bcs*) bends distally in the coxal wall and also falls in line with the pleural suture (*PIS*). The fundamental differences in the two cases, however, are quite apparent: in the grasshopper (fig. 41 B) the outer wall of the coxa itself is divided; in *Panorpa* (fig. 14 A) the meron (*Mer*) is greatly enlarged and is extended into the posterior coxal wall.

The internal ridge of the coxal suture in the prothoracic and mesothoracic legs of *Dissosteira* is continued through the anterior coxo-trochanteral articulation (fig. 36 A, *f*), giving a firm but flexible union between the two articulating segments. The posterior articulation between the coxa and trochanter of the first and second legs consists of a condyle on the trochanter opposed by a concave surface on the coxa, but the two are united by membrane. In the hind leg both coxo-trochanteral articulations consist of opposing processes united by ligament-like thickenings of the articular membrane (fig. 36 D, *f, g*).

*The trochanters.*—The trochanteral segments of the prothoracic and mesothoracic legs have the usual form of the trochanter in insects, each being a short segment articulating as just noted with the coxa, and united distally with the femur. The trochantero-femoral union has an obliquely vertical hinge line and is perhaps slightly movable, since a femoral reductor muscle is present in each of the first and second legs (fig. 36 A, 72). The trochanter of the hind leg is a short ring-like segment (fig. 36 D, *Tr*) expanded on the posterior (mesal) surface, but so narrow externally as to be scarcely perceptible here (fig. 39, *Tr*) between the coxa and the base of the femur. It is immovably connected with the femur but not fused with it, and there is no trochantero-femoral muscle in the hind leg (fig. 39 A). The apodemes of the levator and depressor muscles of the trochanter arise from small sclerites at the base of the trochanter in the dorsal and ventral articular membranes (fig. 36 D).

*The femora.*—In the first and the middle leg the femur is a simple elongate segment (fig. 40, *Fm*) somewhat flattened in its antero-posterior diameter (fig. 36 C). At the distal end of the femur the anterior wall is expanded into a broad lobe that conceals the anterior femoro-tibial articulation (fig. 36 E, *l*); the ventral wall is deeply emarginate and occupied by an ample articular membrane (fig. 36 B) which allows a free flexion of the tibia beneath the femur.

The femur of the hind leg (fig. 39, *Fm*) contains the principal leaping muscles, which are the extensors of the tibiae (135); the hind femur is consequently greatly enlarged and is provided with special structural features. Its length is more than twice that of the middle femur, and its greatest vertical diameter is equal to the length of the prothoracic femur. The flat anterior and posterior surfaces (fig. 39 B) are ridged longitudinally above and below, and the space between is marked by the "fish-bone" pattern of a double series of oblique ridges. The latter separate the lines of attachment of the fiber bundles of the extensor muscles of the tibia on the inner walls of the femur (fig. 39, 135*a*). The distal end of the hind femur (fig. 36 F) is structurally similar to that of the first and second femora (E), but its anterior and posterior walls are strengthened by strongly sclerotized plates.

*The tibiae.*—The tibiae are of similar form and structure in all the legs, each being a slender shaft used as a lever rather than as a container for muscles, and so constructed that it can be folded beneath the femur. The femoro-tibial articulation is a strong dicondylic hinge (fig. 36 E, F, *l*, *m*), and the dorsal lip of the tibial base projects well within the end of the femur to give an efficient leverage to the extensor

muscles (fig. 44). The ventral, flexor muscles are inserted upon an apodeme that arises from a small sclerite in the ventral membrane of the knee joint. The knee mechanism is most strongly developed in the hind leg (figs. 36 F, 39). The base of the tibia here forms a well differentiated articular head bent toward the femur almost at right angles

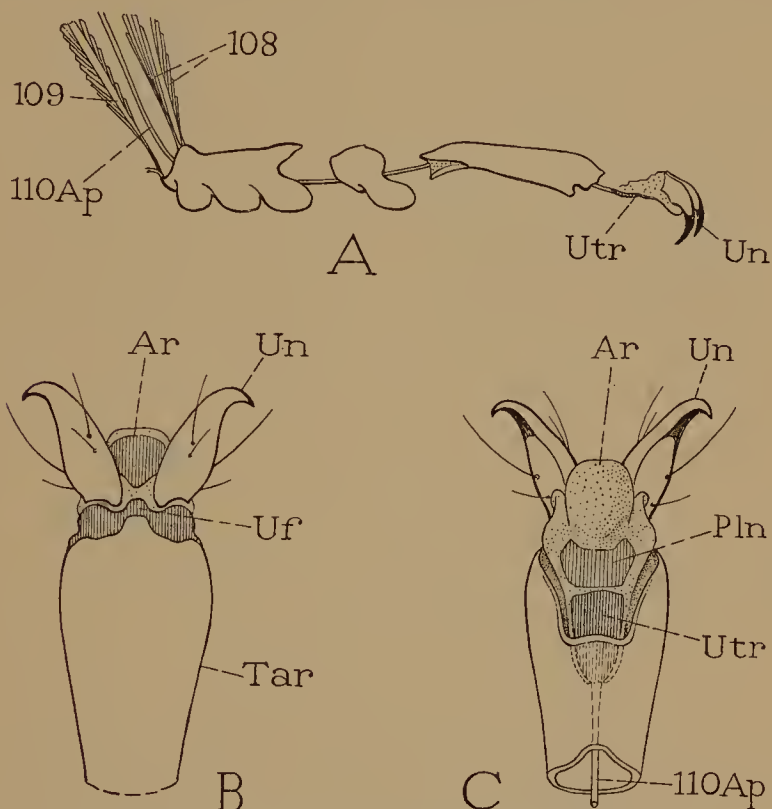


FIG. 42.—Tarsus and pretarsus of *Dissosteira*.

A, tarsus of middle leg disjunct, showing levator and depressor muscles (108, 109) inserted on basal subsegment, and tendon-like apodeme (110Ap) of retractor of claws (Un) arising on unguitractor plate (Utr) and extending through tarsus.

B, dorsal view of distal end of tarsus (Tar), arolium (Ar), and claws (Un), the latter articulated to unguifer (Uf) of tarsus.

C, ventral view of pretarsus and end of tarsus, showing planta (Pln) and unguitractor plate (Utr) in base of pretarsus.

to the length of the segment (fig. 39), and the dorsal lip of the tibial base is produced far into the end of the femur by an inflection of the articular membrane. The first and second tibiae are each provided with two rows of large, flexible, hollow spines on the distal half of the under surface, while the hind tibia has two rows of similar spines on its dorsal surface, but none on the ventral surface except at the end.

*The tarsi.*—The tarsi are each composed of three segment-like pieces (fig. 40, Tar); but the tarsal subdivisions, or articles, are clearly not

segments equivalent to the other parts of the leg, for they are interconnected only by infolded membranes in which there are no sclerotic points of articulation, and none, except the basal one, is ever provided with muscles (fig. 42 A). The large basal subsegment of the grasshopper's tarsus bears three pairs of cushion-like pads on its under surface; the middle subsegment has a single pair; the longer terminal one has no pads. The presence of three pads on the basal subsegment is suggestive that this piece is a composite of three primary tarsal articles. The tarsal pads have been termed *euplantulae* by Crampton (1923).

*The pretarsi.*—The terminal segment in each leg of the grasshopper bears a pair of large lateral *claws* (fig. 42 A, *Un*), but it is itself reduced to a simple median lobe, the *arolium* (B, C, *Ar*), and has two sclerites in its ventral wall (C, *Pln*, *Utr*). The proximal sclerite is the *unguitractor plate* (*Utr*); its base is invaginated into the end of the tarsus and gives attachment to the tendon-like apodeme (*IIoAp*) of the depressor muscle of the pretarsus, known as the retractor of the claws. A levator of the pretarsus is lacking in all insects. The distal ventral sclerite, possibly a subdivision of the unguitractor, is distinguished as the *planta* (*Pln*). The claws arise from the dorso-lateral parts of the base of the pretarsus and are articulated dorsally to the unguifer area on the end of the tarsus (fig. 42 B, *Uf*).

#### MUSCLES OF THE LEGS

The muscles of an insect's leg are comprised in three groups: (1) muscles that move the limb as a whole; (2) muscles that move the telopodite; (3) muscles that move the segments of the telopodite upon each other. The muscles of the first group have their origins entirely within the body; they are inserted on the base of the coxa, on the trochantin, or on apodemes arising in the coxal corium. The muscles of the telopodite arise in the coxa and within the body; they are inserted on the trochanter or on apodemes arising close to the base of the trochanter in the articular membrane of the coxo-trochanteral joint. The muscles of the individual segments of the telopodite beyond the trochanter arise in the segments proximal to their insertions; they are inserted either on the bases of the segments they move or on apodemes arising in the articular membranes.

*Muscles of the leg base.*—The muscles associated with the coxa that move the leg as a whole fall into three groups according to their points of origin; namely, muscles that arise on the tergum, muscles that arise on the sternum, and muscles that arise on the pleuron.



The basal leg muscles arising on the tergum comprise anterior and posterior groups of fibers, or *tergal promotors* (fig. 43 A, *I*) and *tergal remotors* (*J*). The tergal promotors are usually contained in a single muscle, which is inserted on the trochantin (*B*, *Tn*) when this sclerite is present and well developed, otherwise in the articular membrane or on the base of the coxa. The tergal remotors often form a

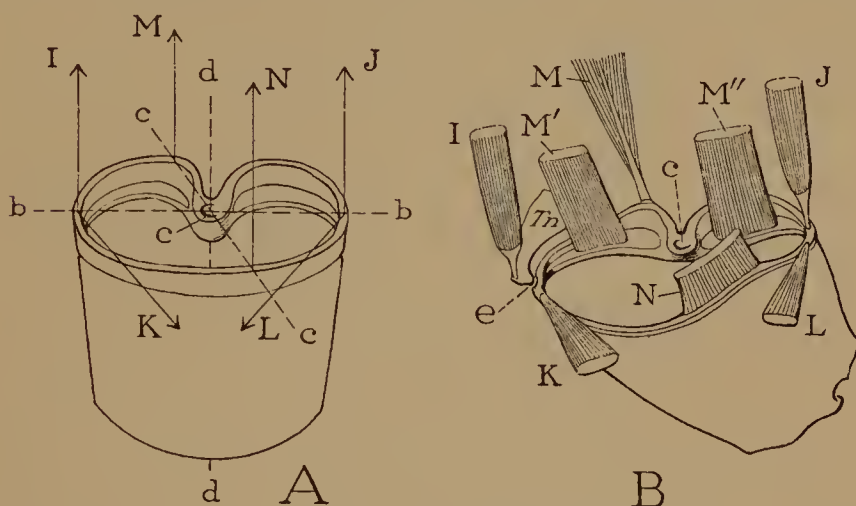


FIG. 43.—Diagrams of the cardinal axes of motion in a coxa articulated to the body by a pleural articulation only, and the coxal musculature in a wing-bearing segment.

A, mechanism of the coxal movements on the pleural articulation (*c*), inner view. The cardinal movements are: (1) *promotion* and *remotion* on a transverse axis (*c c*) by tergal promotor and remotor muscles (*I*, *J*); (2) *rotation* on a vertical axis (*d d*) by anterior and posterior sternal rotator muscles (*K*, *L*); and *abduction* and *adduction* on a longitudinal axis (*b b*) by a pleural abductor muscle (*M*), and a sternal adductor muscle (*N*) arising on sternal apophysis.

B, diagram of typical musculature of a coxa in a wing-bearing segment freely movable on the pleural articulation. *I*, promotor of coxa, tergum to trochantin; *J*, remotor, tergum to coxa; *K*, anterior rotator, sternum to coxa; *L*, posterior rotator, sternum or spinasternum to coxa; *M*, *abductor*, episternum to coxa; *M'*, basalar muscle, basalare to coxa; *M''*, subalar muscle, subalare to coxa (*M'* and *M''* are pleural abductors of coxa in the nymph, fig. 27 C); *N*, adductor, sternal apophysis to coxa.

group of muscles. In *Dissosteira* the tergal promotor is a single muscle for each leg: that of the prothorax (fig. 33 A, 62) is inserted on the trochantin (*Tn*); that of the middle leg is inserted by an apodeme (fig. 37 A, B, C, 89) arising between the trochanter and the coxa; whereas that of the hind leg (fig. 38 A, 118) is attached directly on the anterior angle of the coxa (A, D, F, 118). The tergal remotors of the first leg comprise a group of three muscles (fig. 33 A, B, C, D, 63, 64, 65) inserted on the posterior angle of the coxa; those of the middle leg include two muscles inserted by apodemes on the posterior angle of the coxa (fig. 37 A, B, 90, 91); and those of the hind leg em-

brace two muscles (fig. 38 A, 119, 120) similarly inserted (D, F). The two sets of tergal muscles, promoters and remoters, are clearly antagonists pulling on opposite extremities of the longitudinal basal axis of the coxa (fig. 43 A, *b-b*), the fulcrum of which is at the pleural articulation (*c*).

The sternal musculature of the coxa, when complete, includes three groups of fibers, one inserted on the anterior angle of the coxal base, one on the posterior angle, and one on the mesal rim. The first two are the *anterior* and *posterior rotators* (fig. 43 B, *K, L*) serving to turn the coxa in the plane of its base (*A*) on the pleural articulation (*c*). In the foreleg of *Dissosteira* an anterior rotator is lacking, but there are two posterior rotators (fig. 33 C, 66, 67), the first arising on the base of the sternal apophysis (*SA*), the other on the spina (*1Spn*); both are inserted on the posterior angle of the coxa (*C, D*). The middle leg has a single anterior rotator (fig. 37 A, B, 92) and a single posterior rotator (93), the first arising on the sternellar lobe of the mesosternum (fig. 35, 92), the second (93) on the spina (*2Spn*). In the hind leg there is a single, large two-branched anterior rotator of the coxa arising on the metasternum laterad of the base of the sternal apophysis (fig. 35, 121), and inserted on the anterior angle of the coxa (fig. 38 D, 121); and there are three posterior rotators (figs. 35, 38 E, 122, 123, 124) all arising from the arm of the sternal apophysis.

The mesal sternal muscle of the coxa (fig. 43 B, *N*) is the *adductor*. It pulls upward (*A, N*) on the inner end of the transverse axis (*c-c*) of the coxal base passing through the pleural articulation (*c*). In each segment of *Dissosteira* the coxal adductor arises on the under surface of the arm of the sternal apophysis (figs. 33 C, 69; 37 A, 100, 101; 38 C, D, E, F, 130).

The pleural muscles of the coxa include the functional *abductor* fibers (fig. 43 B, *M*) which directly oppose the adductor (*N*), and, in the wing-bearing segments, two other muscles (*B, M', M''*) that appear to be derived from the primitive abductor system.

In the foreleg of *Dissosteira* the abductor of the coxa is a two-branched muscle (fig. 33 D, 68a, 68b) arising on the inner surface of the invaginated episternum (*Eps*). In the middle leg the abductor group comprises three distinct muscles (fig. 37 A, 94, 95, 96) all arising on the episternum. The first two are inserted by flat apodemes anteriorly on the outer rim of the coxa (*B, C, 94, 95*) and perhaps function here as accessory promoters. The large third muscle (*A, 96*), however, is inserted close before and distinctly laterad of the pleural articulation (*B, c*) by a slender apodeme (96) arising in the coxal corium, and it must be the functional abductor of the coxa. In

the hind leg there are two muscles in the abductor group (fig. 38 C, 125, 126), one being a small anterior muscle (125), apparently accessory to the promotor (A, 118), the other a large posterior muscle (C, 126) which unquestionably functions as an abductor.

The pleural muscles associated with the functional abductor muscles of the coxa in the wing-bearing segments are attached on the outer rim of the coxa (fig. 43 B,  $M'$ ,  $M''$ ) and, in adult insects, arise typically on the epipleural basalar and subalar sclerites (figs. 37 A, 98, 99; 38 B, 128, 129), and function as wing muscles. In some adult insects, as in *Panorpa* (fig. 14 B), the first of these muscles ( $M'$ ) arises on a dorsal lobe of the episternum ( $Ba$ ), which is clearly the homologue of the basalar plate or plates in other insects, such as are present in the adult of *Dissosteira* (fig. 26,  $Ba$ ). The posterior epipleural muscle ( $M''$ ) is always attached to the subalar sclerite in adult insects (figs. 14 B, 37 A, 38 B,  $Sa$ ). Both muscles, however, in the nymph of *Dissosteira* (fig. 27 C,  $M'$ ,  $M''$ ) and in other nymphal Orthoptera, arise directly from the upper edge of the pleuron, one on the episternum, the other on the epimeron, and, if they act together, they must be abductors of the coxa. The epipleural muscles, therefore, appear to be groups of coxal abductor fibers that have become specially developed as secondary wing muscles in the adult. The first is a pronator-extensor of the wing; the second is the depressor-extensor of the wing (fig. 49,  $M'$ ,  $M''$ ).

The foregoing analysis of the basal leg musculature of *Dissosteira* shows that the coxa is provided with six sets of muscles, including an anterior and a posterior group of fibers arising on the tergum (fig. 43 B,  $I$ ,  $J$ ), an anterior and a posterior group arising on the sternum ( $K$ ,  $L$ ), a lateral group arising on the pleuron ( $M$ , and also  $M'$  and  $M''$  in the wing-bearing segments), and a mesal group arising on the sternum ( $N$ ). The anterior and posterior dorsal and ventral muscles may be supposed to represent the theoretical primary tergal and sternal promotors and remoters of a primitive limb basis (fig. 6,  $I$ ,  $J$ ,  $K$ ,  $L$ ), which have become transferred to the coxal region (fig. 11) after the subdivision of the basis into subcoxa and coxa. The lateral and mesal muscles, therefore, are subcoxo-coxal muscles, the fibers of the first ( $M$ ) retaining their origins on the subcoxal pleuron, those of the second ( $N$ ) having been transferred to the sternum, perhaps by the incorporation of the ventral rim of the subcoxa into the definitive sternal plate.

*Muscles that move the telopodite.*—The muscles that operate the telopodite, or that part of the leg beyond the coxo-trochanteral hinge,

comprise the muscles normal to the trochanter, which are a levator and a depressor arising in the coxa (fig. 44, *O*, *Q*), and also special depressor muscles (*P*) that have their origin in various parts of the body segment carrying the leg. The basal lip of the trochanter usually projects into the coxa well beyond the line of the coxo-trochanteral hinge, thereby giving a strong leverage to the depressor muscles inserted upon it.

The branches of the trochanteral depressor arising within the body segment vary much in different insects and in different segments of

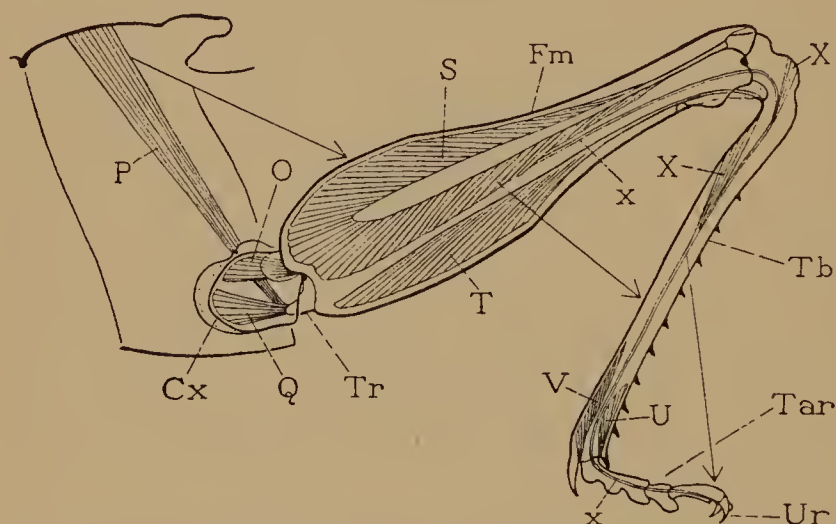


FIG. 44.—Diagram of the mechanism of the hind leg of a grasshopper.

*O*, levator muscle of trochanter, or extensor of telopodite, origin in coxa; *P*, body branch of depressor of trochanter, or flexor of telopodite, origin on tergum; *Q*, coxal branch of depressor of trochanter; *S*, levator of tibia; *T*, depressor of tibia; *U*, levator of tarsus; *V*, depressor of tarsus; *X*, *X*, tibial branches of retractor of claws; *x*, tendinous apodeme of retractor of claws arising on base of unguitractor plate.

the same insect. In the prothorax of *Dissosteira* there are three body branches of the trochanteral depressor, one arising on the episternum (fig. 33 B, 71*b*), the second on the pleural arm (C, 71*c*), and the third on the tergum (B, 71*d*). In the mesothorax there are two body branches of the muscle, both arising on the tergum. In the metathorax a long outer branch and an inner branch (fig. 38 A, 133*c*) arise on the tergum, and a short branch takes its origin on the under surface of the lateral arm of the metasternal apophysis (fig. 38 A, E, 133*d*). These muscles ordinarily serve to lift the body on the legs, but those of the hind legs of the grasshopper are probably accessory to the extensor muscles of the tibiae in the act of leaping (fig. 44, *P*).

*Muscles of the telopodite segments.*—Since the trochantero-femoral joint usually has but little movement in insects, the muscles of the



femur arising in the trochanter are small or absent. In *Dissosteira* a posterior, or reductor, muscle only is present in the trochanter of the first leg (fig. 36 A, 72) and in that of the second leg. In the hind leg there is no movement at the trochantero-femoral joint and femoral muscles are lacking. The usual flexion between the trochanter and the femur of insects is anterior and posterior (production and reduction), and generally only a reductor muscle is present, called the "rotator" of the femur by some writers (Morison, 1927; Weber, 1929).

The femur is occupied mostly by the tibial muscles (fig. 44, *S*, *T*), but it contains also the most proximal branch of the flexor of the claws (*X*). The tibial musculature comprises levator muscles (*S*) and depressor muscles (*T*). In *Dissosteira* there are two levator muscles in each leg, a larger posterior one (fig. 36 E, 106, F, 135), and a very small anterior one (E, 105, F, 134). In the fore and middle legs the depressor of the tibia (fig. 36 B, C, 107) is larger than the levator, and it has a basal branch arising in the trochanter (*B*). In the hind leg the relative proportions of the two muscles are reversed, the posterior levator, or extensor, of the tibia consisting of the great masses of fibers arising on the ridged anterior and posterior walls of the femur (fig. 39, 135*a*, 135*b*), and including smaller branches (135*c*) arising on the dorsal wall in the distal part of the femur. The anterior levator of the tibia in each leg consists of a very slender bundle of fibers arising anteriorly in the base of the femur (fig. 36 A, 73) and inserted by a long, thread-like apodeme on the head of the tibia (E, 105*Ap*, F, 134*Ap*).

The tibiae contain the levator and depressor muscles of the tarsus, and the tibial branches of the flexor of the claws. The tarsal muscles are relatively largest in the fore and middle legs of *Dissosteira*; in the hind leg they occupy only the distal part of the tibia (fig. 39, 137, 138).

The tarsus contains no muscles, the tarsal segments, as before noted, being flexible upon one another but not independently movable. This condition pertains to all insects. The tarsus is traversed by the "tendon," or thread-like apodeme, of the flexor of the claws (figs. 39, 139*Ap*, 44, *x*).

The claws of insects are provided with only a flexor, or retractor, muscle, which is the depressor of the pretarsus (fig. 44 *X*), or the homologue of the depressor of the dactylopodite in arthropods generally. The fibers of the claw muscle arise in several groups in the tibia and femur, and are inserted on a long tendon-like apodeme that arises from the base of the unguitractor plate (fig. 42 C, *Utr*) and

extends through the tarsus and tibia into the femur. In *Dissosteira* two small groups of fibers of the claw muscle arise in the upper part of the tibia (fig. 39, 139*b*, 139*c*), and one arises posteriorly in the base of the femur (fig. 36 A, 78). The pull of the muscles on the tendon retracts the unguitractor plate and flexes the claws ventrally. The extension of the claws probably results from the elasticity of their basal connections and the pressure on the supporting surface.

Typically, the muscles of the pretarsus should arise in the tarsus. It is probable, therefore, that the extension of the fibers into the tibia and femur in insects (and also in chilopods and diplopods) is a secondary condition produced by a proximal migration of the primitive muscle. In Crustacea and Arachnida the pretarsus, or dactylopodite, is provided with levator and depressor muscles, both of which have their origin in the tarsus, or propodite. In some Arachnida there are two pretarsal claws, as in most insects, but the pretarsus has *lateral* articulations with the end of the tarsus, and is provided with dorsal and ventral muscles.

## V. THE WINGS AND THEIR MECHANISM

The wing mechanism of the grasshopper is equally developed in each segment of the pterothorax. The hind wings, though much more extensive than the forewings, or tegmina, and probably the chief organs of flight, have no advantage over the latter except in the stronger development of the flexor apparatus. The forewings, on the other hand, have a more powerful levator equipment than the hind wings because of the presence in the mesothorax of the second pair of tergo-sternal muscles attached dorsally on the scutum (fig. 34, 84). In structure, the hind wings (fig. 45 B) differ from the forewings (A) only in the reduction of the costal area and in the great expansion of the anal area.

### STRUCTURE OF THE WINGS

In general structure, articulation, and mechanism the acridid wings differ little from the wings of other Orthoptera. The tegmina when at rest are flexed over the body in a manner to form a high roof with steeply sloping sides (fig. 50 A,  $W_2$ ) covering the back of the abdomen and inclosing the folded hind wings ( $W_3$ ) in the space above the latter. The anal areas of the tegmina overlap dorsally in a median horizontal plane, the left tegmen being usually on top; the pre-anal areas form the lateral inclines of the tegminal roof. The bend be-

tween the two wing areas takes place along the anal fold (figs. 45 A, 50 A, *AF*), and is produced mechanically during the flexion of the wing. The broad hind wings are folded in a complicated manner, to

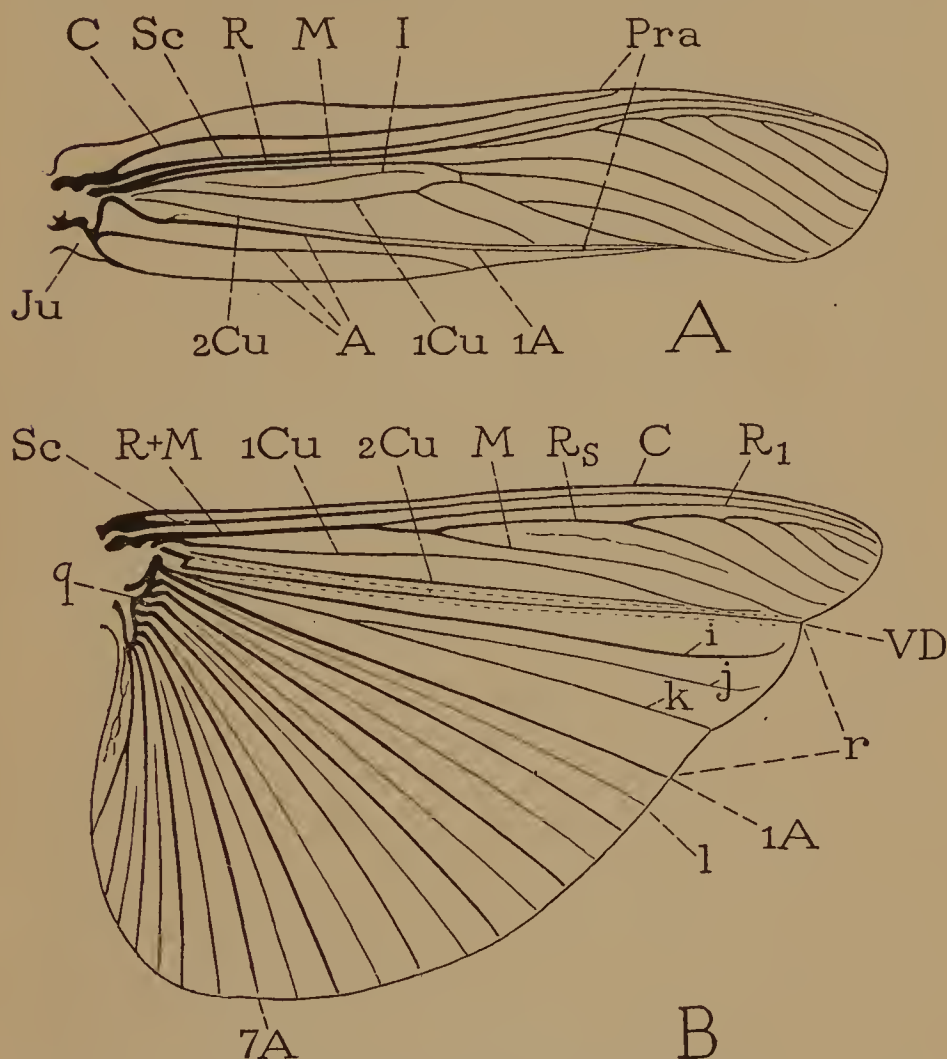


FIG. 45.—The wings and wing veins of *Dissosteira*.

A, fore wing, or tegmen. B, hind wing. A, anal veins, anal area of wing; 1A, first primary anal vein; 7A, seventh primary anal; C, costa; 1Cu, first cubitus; 2Cu, second cubitus; I, intercalary vein; i, j, secondary anal veins of first anal plait; k, first concave anal vein; Ju, jugal area of wing; l, second concave anal vein; M, media; Pra, preanal area of wing; q, basal support of anal veins; R, radius; R<sub>1</sub>, first branch of radius; R<sub>s</sub>, radial sector; r, first anal plait of wing; R + M, united shafts of radius and media; Sc, subcosta; VD, vena divdens.

be described later, and when fully flexed are concealed beneath the overlying tegmina (fig. 50 A).

The area of an insect's wing presents usually three well-defined regions, namely, a *preanal region*, an *anal region*, and a small, pos-

terior, basal region, generally membranous, which Martynov (1925) terms the *jugal region*. The three wing regions are shown in typical form in the forewing of the grasshopper (fig. 45 A). The preanal region (*Pra*) is that lying anterior to the anal fold; the anal region is the region of the anal veins (*A*), the jugal region (*Ju*) is the membranous basal fold of the wing. In many insects the jugal region contains one or two definite veins unconnected basally, or an irregular network of small veins.

The hind wing of the grasshopper (fig. 45 B), and of other insects with similar fan-shaped wings, is usually regarded as differing from the forewing in the great expansion of the anal region. According to Martynov (1925), however, the true anal region of the hind wing in *Acridium* is that part (fig. 45 B, *r*) between the anal fold, or vena dividens (*VD*), and the first vein springing directly from the basal support (*q*) of the anal fan (designated *IA* in fig. 45 B). Three veins (*i*, *j*, *k*), branching from a common base, lie in this region in the wing of *Dissosteira*. The following part of the wing, or that containing the veins attached directly to the basal support (*q*) of the anal fan, Martynov claims is a development of the jugal region of the more primitive type of wing. A jugal area thus developed into a functional wing region he calls the "neala."

Martynov deduces his interpretations of the morphology of the acridid wing from a general study of the wings in other orders of insects. In *Dissosteira*, however, the vein designated *IA* in the hind wing (fig. 45 B) is so clearly the homologue of *IA* in the forewing (*A*), considering the basal relations and the connection with the third axillary sclerite (fig. 47 A, B, *3Ax*), that Martynov's interpretation is not convincing. The area (*r*) of the hind wing (fig. 45 B), lying between *VD* and *IA*, forms the first fold of the anal region (fig. 50 B) in which the vein *k* occupies the position of a "concave" vein at the bottom of the fold, while the two preceding veins (*i*, *j*) strengthen the anterior wall of the fold. The three veins of this region (fig. 45 B, *i*, *j*, *k*) are branches of the first primary anal vein (*IA*). Martynov's general study of the wing regions, however, throws much light on the wing mechanism and morphology.

*Venation of the wings*.—While the venation of the grasshopper's wings is comparatively simple, it is difficult to make a satisfactory interpretation of the homologies of the veins in the posterior parts of the preanal regions. If the relation of the vein bases to the axillary sclerites is taken as a guide to the identities of the veins themselves, the veins of the adult may be named consistently in the two wings, but their relation to the nymphal wing tracheae is not clear in all cases.



The forewing (fig. 45 A) has a broad anterior, or costal, area in which there is no vein represented by a costal trachea in the nymph (fig. 46 A), though the anterior margin is strengthened by a vein-like thickening. The first vein (fig. 45 A, *C*) is evidently the costa branching from the *subcosta* (*Sc*), though the common basal stalk has the usual relation of the subcosta to the first axillary sclerite (fig. 47 A, *1Ax*). The next vein (*R*) is unquestionably the *radius*, as shown by its distal branches and by its basal connection with the second axillary (fig. 47 A, *2Ax*). The *media* (*M*) is united proximally with the radius and with one of the median sclerites of the wing base (*m'*). The first long vein following the media is a two-branched cubitus (*1Cu*), between which and the basal part of the media is the intercalary vein (*I*). Then comes an unbranched vein, here designated *2Cu*, lying close before the anal fold (*AF*), and finally a group of three veins (*A*) connected basally with the third axillary, or flexor sclerite of the wing base (fig. 47 A, *3Ax*).

If we identify the "anal veins" as those veins lying posterior to the anal fold and connected basally with the third axillary, there are then but three anal veins in the forewing of *Dissosteira* (fig. 45 A, *A*, fig. 47 A, *1A*, *2A*, *3A*). An incomplete vein (fig. 47 A, *s*) lying just behind the anal fold (*AF*) is apparently a secondary vein. The vein immediately before the anal fold (*2Cu*) is the "first anal" of the Comstock-Needham system, but probably it is the vein regarded as a part of the cubitus by Tillyard (1919) and others, designated *Cu*<sub>2</sub> by Tillyard and *cubital sector* by Karny. In *Dissosteira* the vein in question has no basal connections and is here termed the *second cubitus* (*2Cu*). It clearly belongs to the cubital area of the wing. In the nymphal wing of an acridid, as illustrated by Comstock and Needham (fig. 46 A), tracheal precursors of the cubitals are not evident, since the final group of three tracheae springing from a common basal stem would appear to represent the group of three anals in the adult wing (fig. 45 A, *A*). According to Comstock (1918), however, the first vein of this group is the "cubitus" (fig. 46 A, *Cu*), and the second the "first anal" (*1A*). The identity between the nymphal tracheae and the adult veins in the forewing is certainly not clear, and no solution of the problem can be offered here.

The vein tentatively called "second cubitus" in this paper (figs. 45 A, 47 A, *2Cu*) is, by nomenclatural priority, the true anal vein, and the name "anal," though a poor designation, should be retained for it, while a new term should be devised for the veins lying posterior to the anal plica associated with the third axillary sclerite. The fan-

like wing region between the anal and jugal plicae might appropriately be called the *vannus* (Latin, fan), and its veins termed the *vannal veins*. This region plays a passive part in flight. The pre-vannal part of the wing is the true remigium (Latin, oar) of the flight mechanism, being the region of the wing directly productive of motion. We might then say that the area of the wing distal to the basal axillary region is divided into a *remigial*, a *vannal*, and a *jugal* region. The separating folds, when present, would then become the *vannal* and the *jugal* plicae. The jugal region expanded is the neala of Martynov.

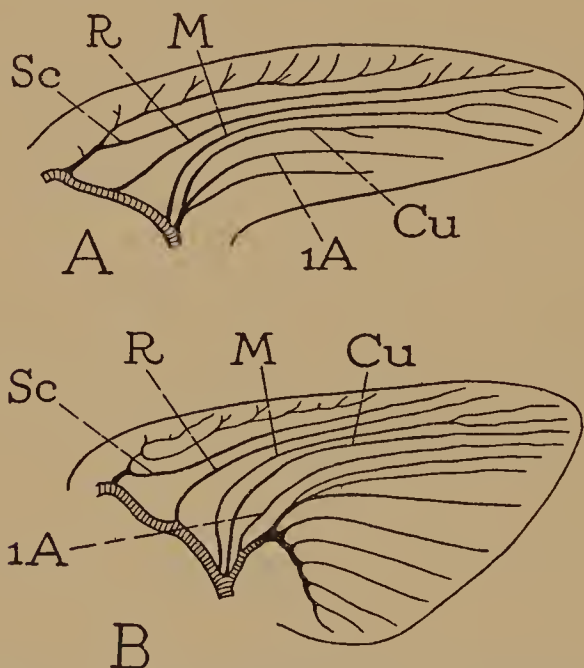


FIG. 46.—Wings of an acridid nymph. (From Comstock, after Comstock and Needham.)

A, fore wing. B, hind wing. The tracheal identifications as given by Comstock and Needham: *1A*, first anal; *Cu*, cubitus; *M*, media; *R*, radius; *Sc*, subcosta.

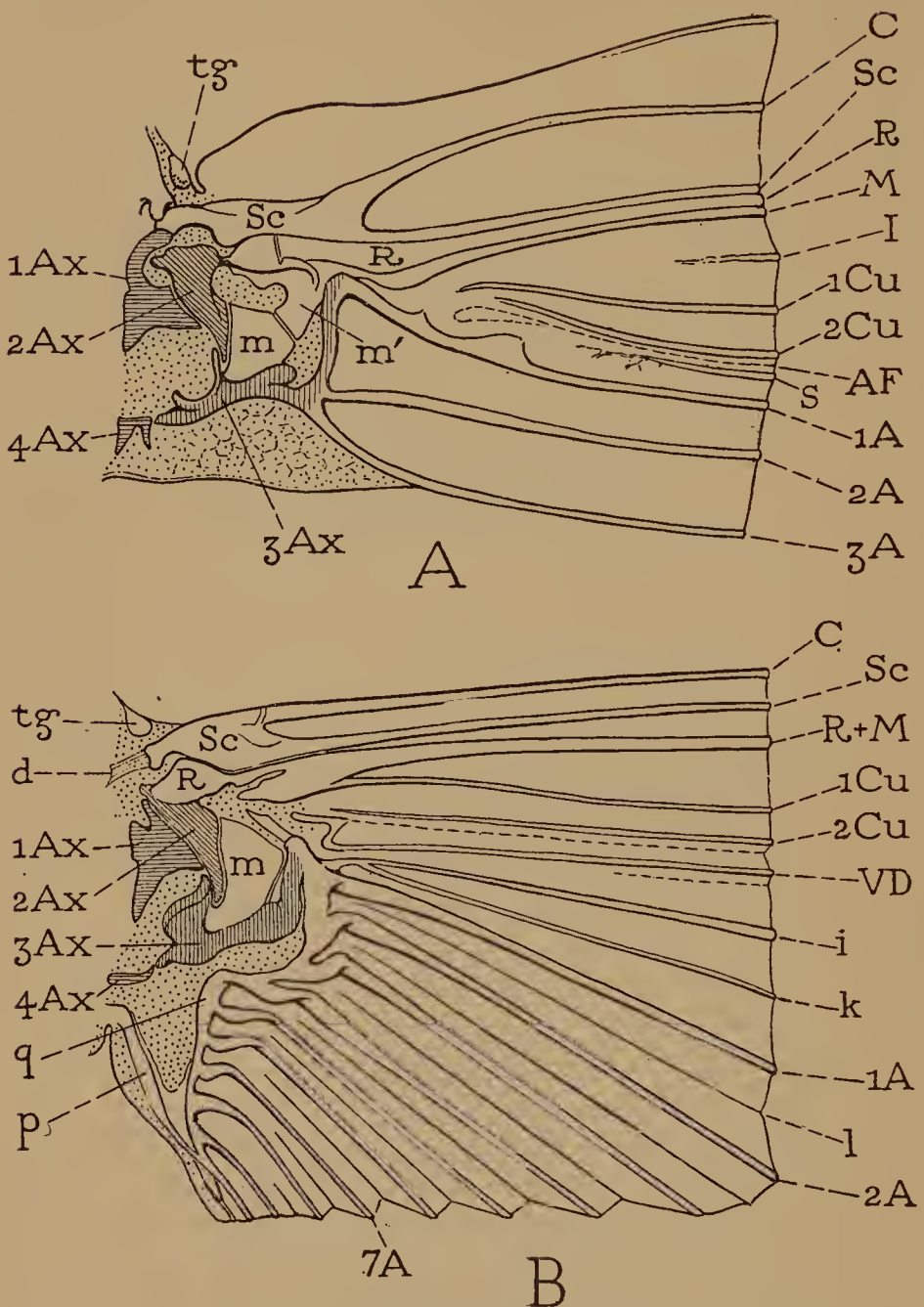
In the hind wing (fig. 45 B) the costa (C) forms the anterior margin of the wing and is united basally with the subcosta (*Sc*). The base of the subcosta (fig. 47 B, *Sc*) does not reach the first axillary sclerite (*1Ax*), evidently by reason of the reduction of the anterior process of the latter, neither does it articulate with the pre-scutal lobe of the tergum (fig. 22 A, *n*), but it is connected with the latter by a ligament-like thickening of the wing membrane (fig. 47 B, *d*). The radius (*R*) is well developed, branched distally, and connected basally with the second axillary (fig. 47 B, *2Ax*). The apparent media is united proximally with the radius; its free part con-

sists of a single branch ( $M$ ) given off from the radial sector ( $R_s$ ). Between the basal radio-medial shaft ( $R + M$ ) and the first anal fold, there are two veins in the cubital area ( $1Cu$ ,  $2Cu$ ); the first (fig. 47 B,  $1Cu$ ) is united proximally with the radio-media, the second ( $2Cu$ ) has no basal connections. In the hind wing, therefore, as in the forewing, there are two distinct cubitals, here named the *first cubitus* ( $1Cu$ ) and the *second cubitus* ( $2Cu$ ). Each of these veins is represented by a trachea in the hind wing of the nymph (fig. 46 B); the first is the "cubitus" ( $Cu$ ) of Comstock, and the second the "first anal" ( $1A$ ). Since both of these veins lie anterior to the anal fold in the adult wing (figs. 45 B, 47 B), however, the writer would agree with Tillyard (1919) that the second is a cubital rather than an anal vein. The orthopteran wing suggests that the second cubitus has the status of an independent vein rather than that of a basal branch of the first cubitus.

The anal fold of the hind wing is double (fig. 50 B), consisting of two plicae, or lines of flexion in the wing membrane, between which lies the *vena dividens* (figs. 45 B, 47 B, 50 B,  $VD$ ). According to Tillyard the *vena dividens* is the "first anal," but since it has no basal connection with the other anals (fig. 47 B), the writer would regard it as a secondary, interpolated vein. The incomplete vein of the forewing lying just behind the anal fold (fig. 47 A,  $s$ ) may represent the *vena dividens* of the hind wing, but it appears rather to correspond with the vein  $i$  of the hind wing (figs. 45 B, 47 B).

The anal veins of the hind wing form a distinct group lying posterior to the anal fold. All the primary anals spring from a basal support (fig. 47B,  $q$ ) which is attached anteriorly to the distal arm of the third axillary ( $3Ax$ ), and which, in the grasshopper, is braced posteriorly by an arm from the tergum (figs. 24, 47 B,  $p$ ). There are ten primary anal veins. A fork from the first ( $1A$ ) divides into three branches ( $i$ ,  $j$ ,  $k$ ) lying in the first lap of the wing that folds beneath the preanal region when the wing is flexed (fig. 50 B). Alternating with the primary, or "convex," anal veins are nine secondary "concave" veins lying in the troughs of the folds between the primary anals, while the vein ( $k$ ) branching from the first anal is the concave vein of the fold between the *vena dividens* and the first anal (fig. 50 B,  $k$ ).

*Articulation of the wings.*—In the membrane of each wing base are four *axillary sclerites*. The first and the fourth (fig. 47 A, B,  $1Ax$ ,  $4Ax$ ) are hinge plates articulating with the edge of the tergum; the second ( $2Ax$ ) is the pivotal sclerite of the wing base; the third ( $3Ax$ )

FIG. 47.—The wing bases of *Dissosteira*.

A, base of tegmen. B, base of hind wing. 1A, 2A, 3A, 7A, first, second, third, and seventh primary anal veins; AF, anal fold; 1Ax, 2Ax, 3Ax, 4Ax, first, second, third, and fourth axillary sclerites; C, costa; 1Cu, first cubitus; 2Cu, second cubitus; d, attachment of base of subcosta to prescutal lobe of tergum; I, intercalary vein; i, secondary vein of first anal plait; k, first concave anal vein; l, second concave anal vein; M, media; m, m', median plates of wing base; p, posterior arm of tergum supporting the anal veins; q, basal support of anal veins; R, radius; R + M, united basal shafts of radius and media; s, secondary vein of fore wing behind anal fold; Sc, subcosta; tg, tegular rudiment; VD, vena divdens.



is the flexor sclerite. In addition to the axillaries there are two plates in the median area of the forewing ( $A, m, m'$ ), and a single median plate in the hind wing ( $B, m$ ).

- The first axillary intermediates between the edge of the tergum and the second axillary, with each of which it is movably connected, and usually, by an anterior process, it articulates with the base of the subcostal vein. The first axillary is confined to the dorsal membrane of the wing base. In the forewing of *Dissosteira* the first axillary (fig. 47 A,  $1Ax$ ) is a flat plate with a narrow anterior process curved outward to meet the base of the subcosta. The sclerite bridges the lateral emargination of the tergum (fig. 22 A,  $Em$ ); its anterior end is supported on the anterior notal wing process ( $ANP$ ), and its posterior part is hinged to the lobe of the scutum ( $o$ ) behind the emargination; its oblique outer margin articulates with the second axillary (fig. 47 A). The first axillary of the hind wing of *Dissosteira* ( $B, 1Ax$ ) is exceptional in the reduction of its anterior process which does not meet the base of the subcosta ( $Sc$ ).

The second axillary presents an exposed surface in both the dorsal and the ventral membranes of the wing base. Its dorsal part forms a triangular plate (fig. 47 A, B,  $2Ax$ ) lying lateral of the first axillary, and closely hinged to the oblique outer margin of the latter; its posterior outer margin articulates with the proximal median sclerite ( $m$ ); to its anterior end is attached the base of the radius ( $R$ ). The ventral part of the second axillary forms a strong, concave plate (fig. 48,  $2Ax$ ) resting by its lower edge on the pleural wing process ( $WP$ ). The second axillary differs somewhat in shape in the two wings of *Dissosteira*, as shown in the figures, but its structure and associations are the same in both.

The third axillary is developed principally in the dorsal wing membrane (fig. 47 A, B,  $3Ax$ ), but it includes also a small sclerotization in the ventral membrane (fig. 48,  $3Ax$ ). The dorsal part of the third axillary (fig. 47) has the form of a strong bar extending outward, in the fully-expanded wing, from the small fourth axillary ( $4Ax$ ) to the anal veins, which latter it supports by an arm bent forward from its distal end. The mesal part of the sclerite bears a strong, elevated process on its anterior margin upon which is inserted the flexor muscle of the wing. Distal to the muscle process, the proximal median plate ( $m$ ) is firmly attached to the third axillary and is functionally a part of it. In the forewing (fig. 47 A) the distal median plate ( $m'$ ) is hinged to the outer margin of the proximal plate.

The fourth axillary (fig. 47 A, B, *4Ax*) is a plate of the dorsal wing membrane only. It is small in each wing and serves merely as a connective between the edge of the tergum and the third axillary. It is probably a detached lobe of the tergum, since it is usually absent in insects that have a posterior notal wing process.

Beneath the base of each wing are the *epipleurites*, or small sclerites derived from the pleuron, which are intimately associated with the wing mechanism in the adult insect. In *Dissosteira* there are in each segment two episternal epipleurites, or *basalares*, (fig. 48, *1Ba<sub>2</sub>*, *2Ba<sub>2</sub>*, *1Ba<sub>3</sub>*, *2Ba<sub>3</sub>*), and a single epimeral epipleurite, or *subalare* (*Sa*). The basalares are hinged to the upper edge of the episternum (*Eps*), and are connected with the subcostal region of the wing base by a ligamentous thickening (*a*) of the ventral wing membrane. The subalare (*Sa*) lies free in the subalar membrane behind the wing process, but it is connected with the ventral plate of the second axillary (*2Ax*) by a thickening (*b*) of the intervening membrane.

#### THE WING MECHANISM

Flying insects are unquestionably descended from wingless ancestors. When paranotal lobes were first evolved on the thoracic segments, the insect was already organized for terrestrial locomotion—there was no provision for future organs of flight. When movable wings were evolved from the paranotal lobes, they had available for their purposes only a motor mechanism developed for other purposes. It needed but an area of flexibility at the base of each paranotal extension to convert the lobe into a movable flap. The dorsal ends of the pleura, previously supporting the bases of the paranotal lobes, easily became fulcra on which the wing flaps could rock up and down. A contraction of the longitudinal muscles of the dorsum could now give a down-stroke to the wing flaps by producing an upward curvature in the tergal plates of the wing-bearing segments, and probably at first the elasticity of the terga sufficed to produce the up-stroke. Thus, apparently, by the simple device of becoming flexible at their bases, the paranotal lobes became wings that could be weakly flapped up and down by the simple motor equipment already at hand.

Modern insects, however, have added much to the primitive wing mechanism. In each of the wing-bearing segments there are powerful tergal-depressor muscles, which, since they do not occur in the prothorax or in the segments of the abdomen, are probably specially developed wing muscles, though they may be supposed to have been evolved from small, lateral tergo-sternal muscles such as are usually

present in the abdomen. Being attached ventrally on the sternum, these muscles indirectly impart a strong up-stroke to the wings by flattening the dorsal curvature of the tergum. The down-stroke of the wings produced by the contraction of the longitudinal dorsal muscles has been strengthened in two principal ways: first, by the obliteration of the secondary intersegmental membranes between the terga, thus eliminating lost motion; and second, by the great enlargement of the dorsal muscles themselves in the wing-bearing segments.

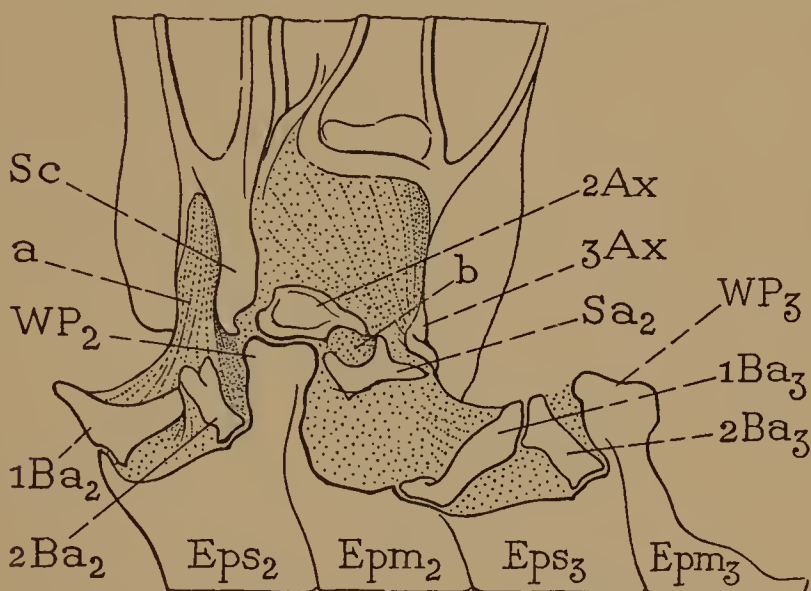


FIG. 48.—Ventral surface of the base of the left tegmen, and upper part the pleuron of *Dissosteira*.

*a*, thickening of membrane uniting basalar sclerites with humeral angle of wing; *2Ax*, ventral plate of second axillary; *3Ax*, ventral plate of third axillary; *b*, connection between subalar sclerite and ventral plate of third axillary; *1Ba*, first basalare; *2Ba*, second basalare; *Sc*, base of subcostal vein; *Sa*, subalare; *WP*, pleural wing process.

The suppression of the intertergal membranes has been accomplished by a fusion between the successive tergal plates, or by a forward extension of the precostal lip of the tergum until it meets the posterior edge of the preceding tergum. Thus are produced the post-notal plates between the mesothoracic and metathoracic terga, and between the metathoracic and first abdominal terga. The enlargement of the dorsal muscles has been accompanied by the development of supporting plates (phragmata) from the ridges of the muscle attachments on the primary intersegmental folds. Furthermore, each tergal plate has been strengthened and better adapted to its function in the flight mechanism by the development of internal ridges, the principal

ones of which are so arranged as to bring the peak of the curvature in the tergum on a transverse line between the wing bases.

The Odonata are commonly said to have a wing mechanism quite different from that of other insects. On the basis of von Lendenfeld's (1881) description of the odonate wing muscles, the dragonflies have been supposed to be equipped with a special set of muscles inserted directly on the wing bases. A study of the thoracic musculature in either the Anisoptera or the Zygoptera, however, will show that there are only two small muscles that can be regarded as special wing muscles; one of these is accessory to the pronator of the wing, the other to the depressor. The large pronator and depressor muscles, though they arise ventrally on the lower edge of the pleuron and are inserted directly on the two basal plates of the wing, are evidently the homologues of the basalar and subalar muscles of other insects. Two smaller muscles lying mesad of the pronator are clearly leg muscles since they have their origins on the coxa and their insertions on the extreme lateral edge of the tergum. Von Lendenfeld ascribed these muscles to the wings; he describes them as arising on the pleuron and as inserted on the wings. Each wing has a homologue of the flexor muscle in other insects, though it does not function as such because of the lack of a flexor mechanism in the base of the odonate wing. The tergo-sternal muscles are highly developed, their ventral attachments are on the sternum and their dorsal attachments on the antero-lateral lobes of the tergum. The dorsal longitudinal muscles are reduced to a pair of small, divergent fiber bundles attached anteriorly on the median apodemal spine of the tergum, and posteriorly on the anterior margin of the following tergum. The wing mechanism of the dragonflies is thus merely an extreme modification of that common to all insects.

A wing, in order to be an efficient organ of progressive flight, must be capable not only of an up-and-down movement, but also of anterior and posterior movements accompanied by a partial rotation on its long axis. The anterior margin of the wing must be brought forward and deflected during the down-stroke, and lifted with a posterior movement during the up-stroke. The rotary movement of the insect's wing is caused partly by the structure of the wing itself and its response to air pressure, and partly by the nature of the wing articulation on the body, but it is greatly augmented by muscles that pull downward on the base of the wing, one before the pleural fulcrum, the other behind it. These muscles are inserted on the basalar and subalar sclerites beneath the wing base (fig. 48, *Ba*, *Sa*). Two of them



are evidently muscles of the leg that have been taken over into the service of the wing, for they are attached ventrally on the coxa (fig. 49,  $M'$ ,  $M''$ ); the other ( $E$ ) arises on the sternum, or in some insects on the pleuron, and is perhaps a specially developed wing muscle. The two muscles of the basalar sclerites ( $E$ ,  $M'$ ) are called *pronators* because they deflect the costal wing margin. The muscle of the subalar sclerite ( $M''$ ) not only deflects the posterior part of the wing, but it acts as a powerful depressor of the entire wing by reason of its connection ( $b$ ) with the ventral plate ( $c$ ) of the second axillary ( $2Ax$ ). These muscles probably also enable the insect to alter its course during flight, and, by changing the plane of the wing movements, to hover in the air, or to fly sidewise or backward.

Finally, most insects have found it advantageous to fold the wings posteriorly over the body. The folding of the wings has involved the development of a mechanism for their flexion and extension. The ability of the wing to be flexed depends upon the mechanism of its axillary region, but the flexing is caused by one or more *flexor muscles* arising on the pleuron and inserted on the third axillary sclerite (fig. 49,  $D$ ). The extension of the wing is produced by the basalar and subalar muscles ( $E$ ,  $M'$ ,  $M''$ ). Considering the other functions of these muscles, the first, therefore, is a *pronator-extensor* of the wing, the second a *depressor-extensor*.

The special features in the mesothorax and the metathorax of the grasshopper that contribute to the mechanism of the wings have been described in Section II of this paper. It was there shown that the fusion of the pleurites and sterna of the mesothorax and metathorax converts these segments into a strong trough-like structure covered dorsally by the two wing-bearing terga. The union of the pleural and sternal elements in the pterothorax is probably a direct adaptation to the leaping function of the hind legs, but the resulting structure also gives a strong framework for the support of the wings and the wing muscles. The tergal plates are separated from the edges of the pleurosternal trough by the ample membranes of the wing bases, and they are thus free to respond to the downward pull of the tergo-sternal muscles. The close union of the terga (fig. 25) and the great size of the dorsal muscles (fig. 34) give efficiency to the latter as elevators of the wings. When the wings are spread they are pivoted on the pleural wing processes by the second axillary sclerites of their bases, and, being closely hinged to the terga by the first and fourth axillaries, they are sharply thrown upward when the tergal plates are depressed, and are turned downward when the terga are elevated.

The mechanism for extending and flexing the wing is highly complex. The muscles that produce the movements of extension and flexion depend for their effect on the details of shape and inter-relationships in the axillary sclerites, on the articulation of the sclerites with the tergum and pleuron, on their connections with the bases of the wing veins, and on the structure of the wings themselves.

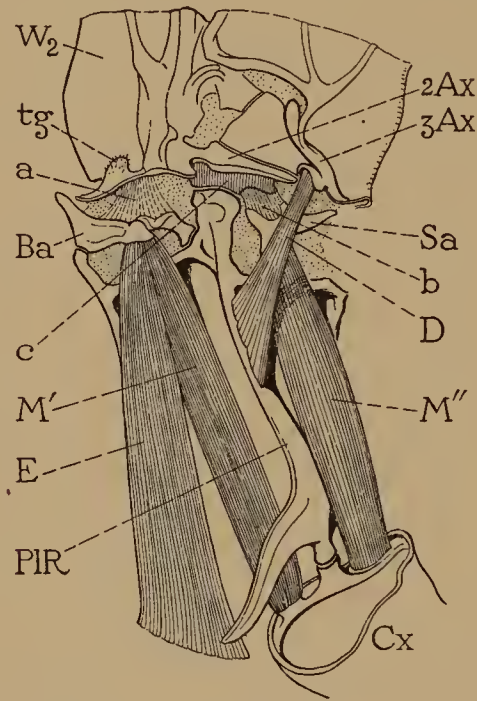


FIG. 49.—The pleural elements of the wing mechanism in the mesothorax of *Dissosteira*.

*a*, thickening of cuticular membrane uniting basalar sclerites with humeral angle of wing (see fig. 48); *2Ax*, second axillary; *3Ax*, third axillary (first and fourth axillaries removed); *b*, thickening of cuticular membrane uniting subalar sclerite (*Sa*) with ventral plate (*c*) of second axillary; *Ba*, first basalare; *c*, ventral plate of second axillary resting on pleural wing process (see fig. 48); *D*, flexor muscle of wing, inserted on third axillary; *E*, pleuro-sternal muscle, or first pronator-extensor of the wing, inserted on basalar sclerite; *M'*, episternal pleuro-coxal muscle, or second pronator-extensor of the wing, inserted on basalar sclerite; *M''*, epimeral pleuro-coxal muscle, or depressor-extensor of the wing, inserted on subalar sclerite; *PIR*, pleural ridge; *Sa*, subalare; *tg*, tegular rudiment; *W<sub>2</sub>*, base of tegmen, showing dorsal surface.

During extension and flexion the wings do not simply turn forward and backward on the pleural wing processes, since each wing is attached to the tergum by its entire basal width. The horizontal movements of the wings are made possible mainly by the flexible lines in the wing bases and by the articulations of the axillary sclerites on one another. The working of the parts involved may be easily observed in a freshly killed specimen if the extended wing is slowly flexed.

In the fully extended wing of *Dissosteira* the axillary sclerites lie approximately flat and in the same plane as the general wing surface (fig. 47 A, B). When the wing is turned posteriorly, however, the axillaries take different positions. In the living grasshopper it is probable that the first movement of flexion is produced by the elasticity of the wing base when the extensor muscles are relaxed, for the wing of a dead specimen automatically assumes a partly flexed position. The fully flexed and folded condition, however, undoubtedly depends on the pull of the flexor muscle (fig. 49, D) on the third axillary.

On the relaxation of the wing, the initial flexing causes the outer end of the third axillary to turn upward, and the pull of the flexor muscle brings this sclerite to a vertical position. The movement of the third axillary turns the attached median plate (*m*) likewise to a vertical position on its hinge with the second axillary (2*Ax*). In the forewing (A), the revolution of the first median plate (*m*) draws the second median plate (*m'*) inward. The second median plate, however, is firmly attached to the united bases of the median, radial, and subcostal veins, and the head of the radius (*R*) is flexibly attached to the anterior end of the second axillary. As a consequence, the movement of the first median plate turns the entire anterior part of the wing posteriorly on the hinge between the radius and the second axillary. But, since the basal connection of this part of the wing forms an oblique line from the head of the first axillary to the articulation between the two median plates, the entire preanal area of the wing is deflected as it turns posteriorly. At the same time, the anal area is lifted but maintains its horizontal plane as the third axillary assumes a vertical position. When the wing finally comes to a longitudinal position over the back, therefore, the anal area is uppermost and the preanal area slants downward on the side (fig. 50 A). During the final revolution of the wing the first axillary turns upward on its hinge with the tergum, the second axillary rotates slightly on the pleural wing process, and the third axillary revolves posteriorly in its vertical position on the fourth axillary.

In the hind wing the mechanism of flexion is in general the same as that of the forewing, but, in addition to the posterior turning of the wing, the great anal area is folded fan-like into many plaits. The third axillary of the hind wing (fig. 47 B, 3*Ax*) is relatively much larger than that of the forewing (A), its muscle process stands out prominently from the shaft, and the flexor muscle inserted on it consists of two bundles of fibers. A distal median plate is lacking in the hind wing, but the single plate (A, *m*) attached to the third ax-

illary affects the anterior group of veins in the same manner as does the corresponding plate of the forewing.

When the distal part of the third axillary is lifted by the pull of the flexor muscle, the median plate turns the preanal area of the wing posteriorly and toward the body, and at the same time deflects it to an almost vertical position, with the costal margin downward. The wing surface makes a double fold along the vena divdens (figs. 45 B, 50 B, *VD*), and the area between the vena divdens and the

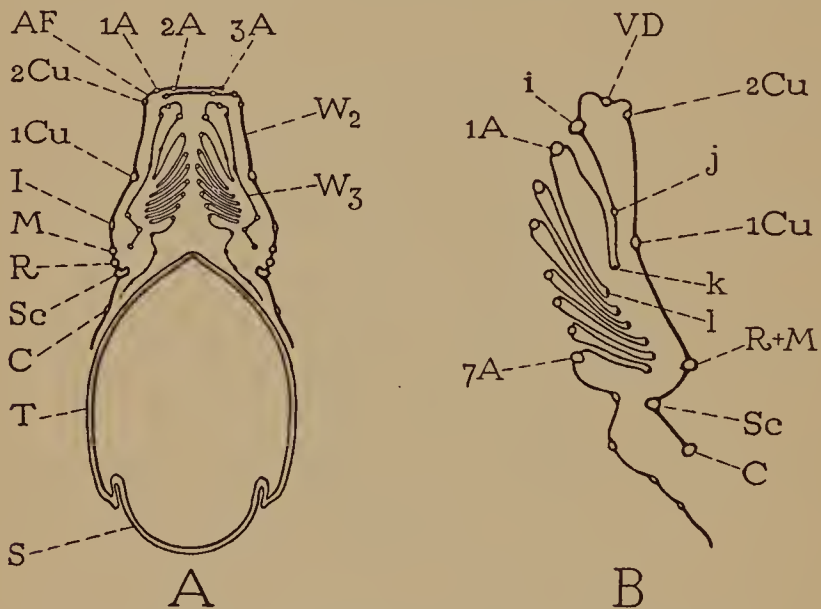


FIG. 50.—Positions of the flexed wings of *Dissosteira*.

A, vertical cross-section through fourth abdominal segment, with wings folded over body, seen from behind. B, section of right hind wing more enlarged.

1A, 2A, 3A, 7A, first, second, third, and seventh primary anal veins; AF, anal fold; C, costa; 1Cu, first cubitus; 2Cu, second cubitus; I, intercalary vein; i, j, secondary veins of first anal plait; k, first concave anal vein; l, second concave anal vein; M, media; R, radius; R + M, combined basal shafts of radius and media; S, sternum; T, tergum; VD, vena divdens.

first principal anal vein (1A) is folded outward beneath the preanal area, with the secondary vein *k* in the ventral angle of the fold (fig. 50 B). While these maneuvers are taking place in the anterior and middle parts of the wing, the anal fan is bent downward as it comes against the side of the abdomen, and its ventral surface is turned outward beneath the deflected preanal area. The membrane of the fan is plaited between each two of the first seven principal anal veins (fig. 50 B, 1A-7A), with the secondary veins occupying the ventral lines of the folds. The posterior part of the fan spreads out against the upper part of the side of the abdomen (A).



A careful study of the forms of the folded wings of the grasshopper, as seen in transverse section (fig. 50), will suggest that many details of structure, both in the tegmina and in the hind wings, are adaptations to the passive state of flexion rather than to the active phases of flight.

The extension of the wings is effected probably by the action of both the basalar and the subalar muscles (fig. 49 *E*, *M'* and *M''*). The basalar sclerites (fig. 48, *1Ba*, *2Ba*) are connected by a tough membranous fold (*a*) with the base of the wing anterior to the wing process. A depression of these sclerites on their episternal articulations, caused by the contraction of their muscles (fig. 49, *E*, *M'*), must therefore release the flexed wing from its position over the body and turn it outward. The principal extensor of the wing, however, appears to be the muscle of the basalar sclerite (fig. 49, *M''*). In the flexed wing, the second axillary sclerite is elevated between the first axillary on the one hand, which now stands in a vertical plane on its tergal hinge, and the median plate (*m*) on the other, which rises vertically from its hinge on the second axillary. The ventral plate of the second axillary is connected with the subalar sclerite by a thickening of the intervening membrane (figs. 48, 49, *b*). The downward pull of the basalar muscle (fig. 49, *M''*) is therefore exerted on the second axillary. It is easy to demonstrate that a downward pressure on the second axillary flattens the entire wing base by restoring the first axillary, the median plate, and the third axillary to the horizontal plane, and thereby extends the wing.

When the wings are extended, the mechanism of flight becomes operative. This includes the direct and indirect muscles, which accomplish the movements of levation, depression, and rotation, and which have already been described.

## VI. THE SPIRACLES

The generalized ancestors of modern insects possibly had a pair of tracheal invaginations on each of the 17 body segments between the primitive head, or procephalon, and the periproct. Evidence of the existence of such invaginations has been found, however, on only 14 segments, namely, the second maxillary segment, the three thoracic segments, and the first ten abdominal segments.

Tracheal invaginations of the second maxillary segment have been reported by Nelson (1915) to be present in the embryo of the honeybee. They arise, Nelson says, on the lateral surfaces of the anterior half of the segment above the bases of the rudiments of the second

maxillae, shortly behind the boundary between the first and second maxillary segments. The second maxillary spiracles have thus the same relative position on their segment as have all the body spiracles in the embryo, or the abdominal spiracles in adult insects. The embryonic invaginations of the labial segment, according to Nelson, give rise to a part of the tracheal system of the head, but are later closed and leave no external trace of their existence in the adult insect.

Prothoracic spiracles are known to exist as functional organs of the adult only in some of the Sminthuridae (Collembola). They are situated laterally in the neck membrane close to the posterior margin of the head, but Davies (1927) claims that the region bearing the spiracles belongs to the prothorax. These cervical or prothoracic spiracles are the only spiracles present in the Sminthuridae, and no other collembolan is known to possess either spiracles or tracheae in any part of the body. Temporary prothoracic spiracles, followed by the usual series of spiracular invaginations, have been described in the embryo of *Blattella* by Cholodkowsky (1891), and in the embryo of *Leptinotarsa* by Wheeler (1889).

The usual first pair of thoracic spiracles of adult, nymphal, and larval insects is always situated either in the posterior part of the prothorax or in the intersegmental membrane between the prothorax and the mesothorax. In the embryos of most insects, however, these spiracles are said to lie anteriorly in the mesothorax; they would appear, therefore, to be the true mesothoracic spiracles which have become prothoracic in position by a secondary forward migration. The usual second pair of adult thoracic spiracles are the embryonic metathoracic spiracles, and they sometimes occur on the anterior part of the metathorax in the adult, though more commonly they lie in the membrane between the mesothorax and the metathorax, or in the posterior part of the mesothorax. The segmental relations of the thoracic spiracles is somewhat complicated by the fact that the muscles of their closing apparatus have their origins in the segments on which the spiracles are situated in the adult. Since, however, the musculature of the thoracic spiracles is not alike in different groups of insects and is often different in the two spiracles of the same insect, it is probably of secondary development in all cases.

Contrary to the embryological evidence of the segmental relations of the spiracles, there are many points in the anatomy of the tracheal system, and in the innervation of the spiracular muscles, that suggest, as now claimed by several writers, that the spiracles are primarily intersegmental invaginations, and that their definitive positions are

the result of migrations either forward or rearward into the segmental regions of the body.

The abdominal spiracles are situated, with few exceptions, on the anterior lateral parts of the abdominal segments, where they lie in the tergal plates, between the terga and the sterna, or in the edges of the sterna. There are usually eight pairs of abdominal spiracles in adult and larval insects, though the number may be variously reduced. There is evidence, however, of more than eight spiracles having been present on the abdomen of primitive insects. Cholodkovsky (1891) reports the existence of a pair of tracheal invaginations on the first nine abdominal segments of *Blattella*, and Heymons (1897) says there are apparent rudiments of spiracles on the tenth abdominal segment of *Lepisma*. In certain insects the spiracles of the first abdominal pair are situated very close to the base of the metathorax, and long discussions recur as to whether these spiracles belong to the thorax or to the abdomen. In all cases, however, it will be found that the spiracles in question lie posterior to the third phragma, which marks the intersegmental line between the metathorax and the first abdominal segment, or behind the lateral extensions of the postnotal plate in the metathorax. The spiracles are therefore abdominal, as is shown also by the destination of their tracheae.

The external aperture of a spiracle may be a simple opening leading directly from the exterior into the trachea. In most cases, however, there is a pre-tracheal chamber, or *atrium* (fig. 53 A, B, *Atr*), formed by an inflection of the body wall, from the inner end of which arises the trachea (*Tra*). The atrium of the spiracle, therefore, appears to be a secondary invagination of the body wall, which has carried the mouth of the original tracheal invagination to a more protected position beneath the surface. In some cases the edges of the atrial orifice are elevated to form a pair of protruding lips guarding the entrance (fig. 53 A, *c*, *d*), in others the opening is fringed with opposing brushes of hairs, usually thickly branched, or it is itself reduced to a very small diameter.

Spiracles are usually provided with a closing apparatus. In the Apterygota the spiracles are said to lack an occlusor mechanism (Du Buisson, 1926; Davies, 1927), and the thoracic spiracles of Plecoptera are simple apertures giving open passages into the tracheae. In general, however, the spiracles have either a device for closing the outer lips of the atrial chamber, or an apparatus for blocking the passage from the atrium into the tracheae. The occlusor mechanism of the abdominal spiracles is of the second type; that of the thoracic

spiracles may be of similar structure (caterpillars and other larvae), but usually the closing apparatus of the thoracic spiracles in adult insects effects a movement of one or both of the outer lips of the atrial chamber.

The Acrididae possess the two usual pairs of thoracic spiracles and eight pairs of abdominal spiracles. The first thoracic spiracle on each side is situated laterally in the ample intersegmental membrane between the prothorax and the mesothorax (fig. 20 B, 26,  $Sp_2$ ) where it is covered externally by the lateral part of the large posterior fold of the protergum (fig. 20 B,  $Rd$ ). The second spiracle lies in the posterior ventral angle of the mesothoracic epimeron just above the base of the middle leg and immediately before the intersegmental groove between the mesopleuron and the metapleuron (fig. 26,  $Sp_3$ ). The abdominal spiracles are carried by the first eight abdominal terga, each being placed in the lower anterior angle of the corresponding tergal plate. The first of the series, therefore, lies in the tympanal cavity of the first segment, where it is situated on the small triangular area before the tympanal membrane and just in front of the support of the chordotonal organ. All the spiracles are well developed, and each is provided with an efficient closing apparatus, the mechanism of which presents the usual two types of structure, the first pertaining to the thoracic spiracles, the second to the abdominal spiracles. The details of structure, however, are quite different between the two thoracic spiracles.

*The first thoracic spiracle.*—The first spiracle of the thorax of *Dissosteira carolina* is contained in a small, irregular plate, or *peritreme* (fig. 51 A, *Ptr*), lying laterally in the intersegmental membrane between the prothorax and mesothorax (fig. 20 B,  $Sp_2$ ), covered externally by the overlapping fold of the protergum. The lower end of the peritreme is produced posteriorly and upward in a small, free process (fig. 51 A, *a*), bearing on its base a flat-topped, pale-colored tubercle (*b*) projecting outward. The tubercle is a little higher than the lips of the spiracle and evidently serves as a stop to prevent the covering flap of the protergum from resting too closely against the spiracle. The spiracular opening is an obliquely vertical slit with a slight italic curve and strongly protruding anterior and posterior lips (*c*, *d*). The length of the slit is about 0.60 mm. in the male grasshopper, and about 0.75 mm. in the female. The anterior lip (*c*) is a rigid elevation of the wall of the peritreme; its inner face is soft and deeply grooved parallel with the outer edge. The posterior lip (*d*) is a weaker and freely-movable flap, but it has a sharp,



strongly-sclerotized marginal band (*e*) which, when the spiracle is closed, fits into the groove of the anterior lip.

The cleft of the first spiracle opens into a shallow atrium from which are given off two tracheae, a larger dorsal one (fig. 51 B, *f*) and a smaller ventral one (*g*). From without, therefore, the first spiracle appears to have a double opening (A, *f*, *g*). In some of the Orthoptera that have tympanal organs on the front legs, the trachea of the ventral (or posterior) opening of the spiracle appears to have become specialized as an "acoustic" trachea since it goes only to the

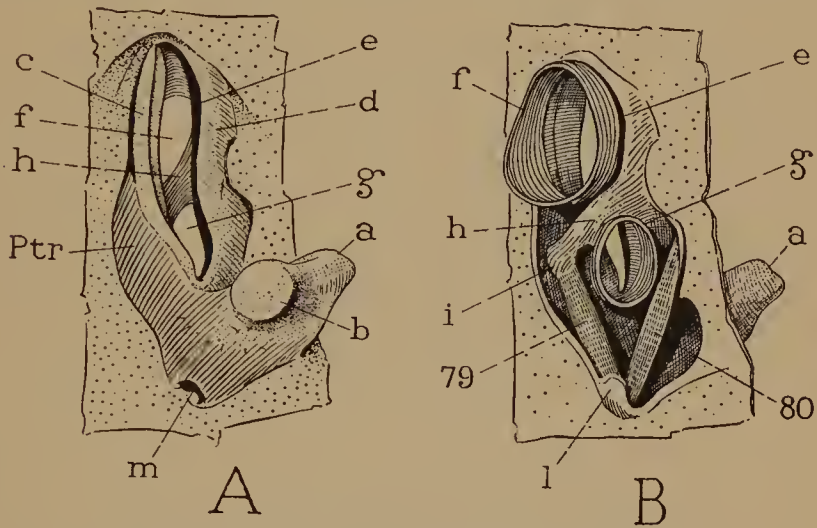


FIG. 51.—First thoracic spiracle of *Dissosteira*.

A, outer view of left spiracle. B, inner view of right spiracle. *a*, ventral lobe of peritreme; *b*, process of peritreme protecting spiracle from covering flap of pronotum; *c*, anterior lip of spiracle; *d*, posterior lip of spiracle; *e*, hard edge of posterior lip; *f*, dorsal trachea; *g*, ventral trachea; *h*, internal lever of posterior lip forming a septum between the tracheae; *i*, head of lever on which closing muscle (79) is inserted; *l*, ventral internal process of peritreme on which spiracular muscles arise; *m*, external pit forming internal process *l*; *Ptr*, peritreme; 79, opening muscle; 80, closing muscle.

front leg, where it branches into the two tracheae of the tympanal organ. This fact led Graber to the conclusion that the double structure of the first spiracle in Orthoptera originated from the separation of an "acoustic" trachea from the general respiratory tracheae of the prothorax. Carpentier (1924, 1925), however, has shown that the double first spiracle is a character of Orthoptera in general, whether tympanal organs are present in the front legs or not, and that in most forms the tympanal trachea is not isolated from the rest of the respiratory system. The specialization, he says, is carried to its highest degree in the tettigoniid *Phasgoneura viridissima*, where the spiracular orifice of the leg trachea is enormously enlarged. Here, ap-

parently, is a case of an advantage derived by a specific organ from a general structure first developed for some other reason.

In the septum between the two spiracular openings in *Dissosteira* (fig. 51 A, *h*) is a strong internal bar (B, *h*) projecting anteriorly and ventrally from the posterior lip of the spiracle, and terminating in a free process (*i*) that extends anterior to the spiracular opening. Upon this process is inserted a short muscle (79) which has its origin ventrally on an inner process (*l*) of the lower angle of the peritreme, the site of which is marked externally by a pit (A, *m*). A second muscle (B, 80) arises from the base of the same process (*l*) and extends dorsally and posteriorly to its insertion on the base of the posterior lip of the spiracle behind the ventral trachea. The first muscle (79) is the occlusor of the spiracle; the second (80) is evidently its antagonist. A downward pull on the head of the septal arm (*i*), where the anterior muscle is inserted, closes the spiracle by rotating the movable posterior lip forward on its dorsoventral axis and bringing thus its sharp free edge into the groove of the anterior lip. Conversely, a downward pressure on the base of the posterior lip, at the point where the posterior muscle (80) is inserted, rotates the lip in the reverse direction and opens the spiracle. The differential action of the two muscles results from the opposition of their two points of insertion on either side of the long axis of the posterior lip, and is accentuated by the difference in their points of origin on the ventral process (*l*) of the peritreme. Vinal (1919), Lee (1925), and other writers have regarded both muscles of the first spiracle in Acrididae as occlusors.

*The second thoracic spiracle.*—The second thoracic, or metathoracic, spiracle of *Dissosteira* is located in the lower, posterior angle of the mesothoracic epimeron of the adult (fig. 26, *Sp*<sub>3</sub>), where it is surrounded by a narrow membranous area (fig. 52 A, *mb*). Externally this spiracle presents two thick, elongate oval, valve-like lips, (fig. 52 A, *c*, *d*) separated by a sinuous vertical cleft having a length of about 0.50 mm. in the male insect. Both lips of the second spiracle are movable, though they are united ventrally in a broad lobe (*n*). The spiracular lips stand out prominently from the body wall (fig. 53, A, *c*, *d*), and between them is a shallow atrium (*Atr*) from which arises a single large trachea (*Tra*) that soon divides into a dorsal and a ventral branch. The closing mechanism of the second spiracle includes but a single short occlusor muscle (fig. 52 B, *III*). The muscle arises ventrally from a small process (*o*) on the posterior dorsal margin of the mesocoxal cavity, and is inserted on the ventral

lobe (*n*) of the spiracle. There is no special device for opening this spiracle; the lips diverge by their own elasticity, as is shown by the fact that the spiracle is always open in a dead insect. The occlusor muscle brings the edges of both lips together.

*The abdominal spiracles.*—The eight spiracles of the abdomen in *Dissosteira* are quite different from either of the thoracic spiracles. They are not provided with projecting external lips (fig. 53 B), the body wall being directly inflected in each spiracle to form an open atrial chamber (*Atr*). The atrium leads by a narrowed aperture at

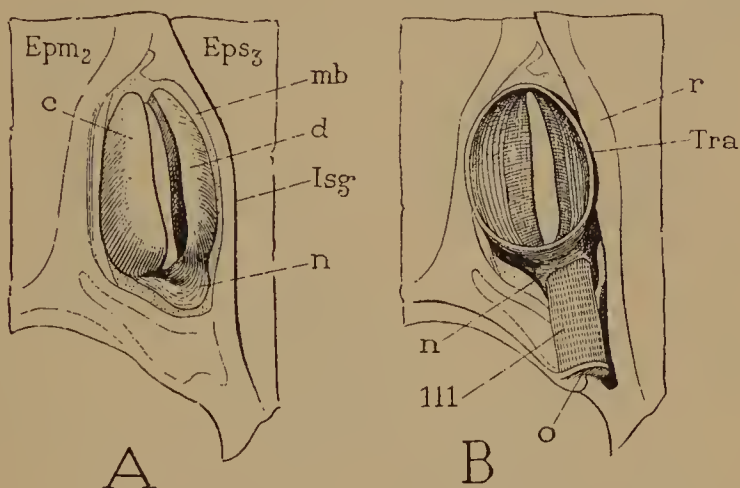


FIG. 52.—Second thoracic spiracle of *Dissosteira*.

A, outer view of left spiracle. B, inner view of right spiracle. *c*, anterior lip of spiracle; *d*, posterior lip of spiracle; *Epm<sub>2</sub>*, epimeron of mesothorax; *Eps<sub>3</sub>*, episternum of metathorax; *Is<sub>g</sub>*, intersegmental fold; *mb*, membrane surrounding spiracle; *n*, ventral lobe of spiracle uniting the lips and giving insertion to spiracular muscle (*III*); *o*, internal lobe on rim of coxal cavity on which spiracular muscle arises; *r*, internal intersegmental fold; *Tra*, trachea; *III*, closing muscle of spiracle.

its inner end into the spiracular trachea (*Tra*), and the occlusor mechanism regulates this opening.

The longer axis of the first abdominal spiracle is obliquely horizontal (fig. 54 A) with the anterior end a little higher than the posterior. The other spiracles (C, D) are placed more nearly vertical, so that the dorsal end of each corresponds with the anterior end of the first spiracle. In each spiracle one wall of the atrium is rigid (fig. 53 B, *t*), and the other (*s*) is movable. The rigid wall is dorsal in the first spiracle (fig. 54 A, *t*) and posterior in the other spiracles (C, D). It is strengthened by a thickening in the external body wall (figs. 53 B, 54 A, *u*) from which it is inflected. The movable wall of the atrium (*s*), which is ventral in the first spiracle (fig. 54 A)

and anterior in the others (C, D), is flexible because the body wall immediately external to it is weak, and because the two end walls of the atrial chamber are membranous. The posterior or ventral end of the movable wall is produced into a long, free manubrium (fig. 54 B, D, *q*) that projects into the body cavity and gives attachment to two muscles, one dorsally, the other ventrally. These muscles, acting antagonistically, either close or open the passage from the atrium into the trachea (fig. 53 B) by means of their attachments on the movable wall of the atrium.

The short dorsal muscle of the first abdominal spiracle (fig. 54 B, *CMcl*) arises on the rim of the tympanum (*p*) above the spiracle;

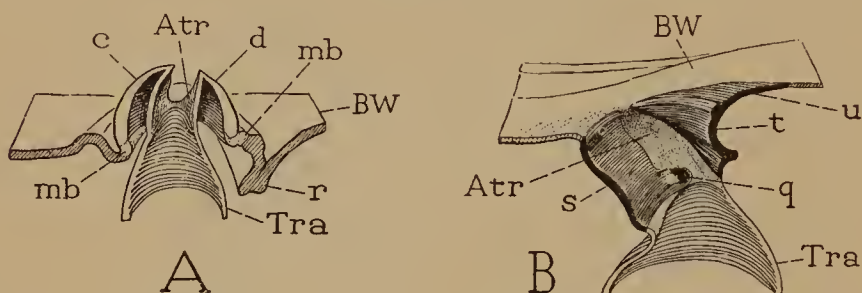


FIG. 53.—Sections of spiracles of *Dissosteira*.

A, longitudinal section through second thoracic spiracle, showing anterior and posterior lips (*c*, *d*) as projecting folds of body wall (*BW*) inclosing an atrium (*Atr*), or entrance to trachea (*Tra*).

B, vertical section through first abdominal spiracle, showing direct inflection of body wall to form atrial chamber (*Atr*), of which anterior wall (*s*) is movable, and posterior wall (*t*) immovable.

*Atr*, atrium; *BW*, body wall; *c*, anterior lip of spiracle; *d*, posterior lip of spiracle; *mb*, membrane surrounding lips of spiracle; *q*, manubrium or muscle process of ventral wall of atrium; *r*, intersegmental fold; *s*, ventral wall of atrium; *t*, dorsal wall of atrium; *Tra*, trachea; *u*, plate in tergal wall supporting dorsal wall of atrium.

the long, slender ventral muscle (*OMcl*) arises ventrally on an inflection of the integument mesad of the hind coxa and posterior to the triangular coxal plate of the metasternum (fig. 30 A, *t*). It is easy to demonstrate that the dorsal muscle (fig. 54 B, *CMcl*) is the closer of the spiracle and the ventral one (*OMcl*) the opener. A dorsal pull upon the manubrium (*q*) of the movable ventral wall of the atrium (*s*) brings the inner edge of the latter against the inner edge of the fixed dorsal wall (*t*) and thus closes the passage from the atrium into the spiracular trachea. By a counter movement the passage is opened.

The mechanism of the other abdominal spiracles is the same as that of the first. The short, fan-shaped occlusor muscle (fig. 54 C, D,



*CMcl*) arises on the wall of the tergum immediately behind the spiracle, and is inserted on the manubrium of the movable wall of the atrium (*q*), which projects ventrally and posteriorly. The long opening muscle (*OMcl*) arises on the lateral edge of the corresponding sternum and extends posteriorly and dorsally to its insertion on the manubrium.

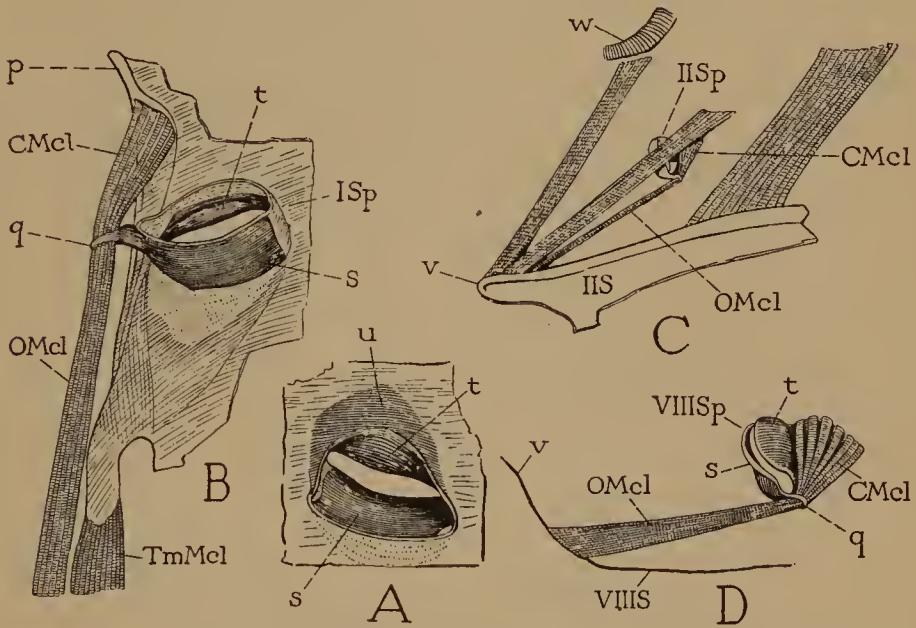


FIG. 54.—Abdominal spiracles of *Dissosteira*.

A, first abdominal spiracle, left, outer view. B, inner view of the same spiracle, showing muscles. C, second abdominal spiracle, right, inner view, with tergo-sternal muscles of second abdominal segment. D, eighth abdominal spiracle, right, inner view.

*CMcl*, closing muscle of spiracle; *ISp*, first abdominal spiracle; *IIS*, second abdominal sternum; *IISp*, second abdominal spiracle; *OMcl*, opening muscle of spiracle; *p*, anterior margin of tympanal cavity; *q*, manubrium of ventral or anterior wall of atrial chamber; *s*, movable ventral or anterior wall of atrial chamber; *t*, fixed dorsal or posterior wall of atrial chamber; *u*, thickening of tergal wall supporting dorsal or anterior wall of atrial chamber; *v*, anterior apodermal arm of abdominal sternum; *VIIIS*, eighth abdominal sternum; *VIIISp*, eighth abdominal spiracle; *w*, posterior angle of tympanal cavity.

The grasshoppers are abdominal breathers. A discussion of the mechanism of respiration would, therefore, lead too far beyond the anatomical limits of the present paper. Recent studies on the breathing of Orthoptera give such varied and conflicting results that we must conclude either that the subject still needs a critical investigation or that the insects have no fixed methods of respiration. The weight of evidence is rather in favor of inconsistency on the part of the insects.

## ABBREVIATIONS USED ON THE FIGURES

- A*, Anal veins. *1A*, *2A*, etc., first anal, second anal, etc.  
*Ac*, antecosta.  
*acs*, antecostal suture.  
*Acx*, precoxal bridge.  
*AF*, anal fold.  
*ANP*, anterior notal wing process.  
*Ap*, apodeme.  
*Ar*, arolium.  
*Atr*, atrium.  
*Aw*, prealar arm of tergum.  
*Ax*, axillary sclerite. *1Ax*, *2Ax*, *3Ax*, *4Ax*, first, second, third, and fourth axillaries.  
*AxC*, axillary cord.  
  
*Ba*, basalare.  
*Bc*, basicosta, basal ridge of coxa.  
*bcs*, basicostal suture of coxa.  
*Bcx*, basicoxite.  
*Brn*, branchia, gill.  
*Bs*, basisternum.  
*BW*, body wall.  
  
*CMcl*, closing muscle of spiracle.  
*cpl*, supra-coxal plate of subcoxa.  
*Cu*, cubitus. *1Cu*, *2Cu*, first and second cubitus.  
*Cv*, cervix, neck.  
*1cv*, *2cv*, first and second lateral cervical sclerites.  
*Cx*, coxa.  
*CxC*, coxal cavity.  
*CxP*, pleural coxal process.  
*Cxpd*, coxopodite.  
*cxs*, coxal suture.  
  
*D*, flexor muscle of wing.  
*DMcl*, dorsal longitudinal muscles.  
  
*E*, basalar-sternal muscle.  
*Em*, lateral emargination of tergum.  
*Endp*, endopodite.  
*Epm*, epimeron.  
*Eppd*, epipodite.  
*Eps*, episternum.  
*Eupl*, eupleuron.  
*Eutn*, entrochantin.  
*Expd*, exopodite.  
  
*Fm*, femur.  
*Fu*, furca.  
  
*H*, head.  
  
*I*, intercalary vein.  
tergal promotor muscle of coxa.  
*I-XI*, abdominal segments.  
*IS-XIS*, abdominal sterna.  
*Isg*, intersegmental fold.  
*ISp*, *IISp*, first and second abdominal spiracles.  
*Ist*, intersternite.  
*IT-XIT*, abdominal terga.  
  
*J*, tergal remotor muscle of coxa.  
*Ju*, jugal area of wing.  
  
*K*, sternal promotor, anterior rotator of coxa.  
  
*L*, leg.  
sternal remotor, posterior rotator of coxa.  
*LB*, leg basis.  
*Ls*, laterosternite.  
  
*M*, media.  
abductor muscle of coxa.  
*m*, *m'*, distal median plates.  
*M'*, basalar-coxal muscle.  
*M''*, subalar-coxal muscle.  
*Mb*, secondary intersegmental membrane.  
*mb*, membrane.  
*Mer*, meron.  
  
*N*, *N'*, adductor muscle of coxa.  
  
*O*, levator muscle of trochanter.  
*OMcl*, opening muscle of spiracle.  
  
*P*, body branch of depressor muscle of trochanter.  
*PaR*, parapsidal ridge.  
*pas*, parapsidal suture.  
*Pc*, precosta.

- Pcx*, precoxal bridge.  
*Ph*, phragma. *1Ph*, *2Ph*, *3Ph*, first, second, and third phragmata.  
*Pl*, pleuron.  
*pl*, pleural sclerites between tergum and subcoxa.  
*PLA*, pleural apophysis.  
*Pln*, planta.  
*PLR*, pleural ridge.  
*PLS*, pleural suture.  
*PN*, postnotum.  
*PNP*, posterior notal wing process.  
*Poc*, postocciput.  
*PoR*, postoccipital ridge.  
*Ppct*, prepectus.  
*Ppt*, periproct.  
*PR*, prescutal ridge.  
*Pra*, preanal area of wing.  
*Ps*, presternum.  
*ps*, prescutal suture.  
*Psc*, prescutum.  
*PT*, posterior arm of tentorium.  
*Ptar*, pretarsus.  
*Ptr*, peritreme.  
*Pze*, postalar arm of postnotum.  
  
*Q*, coxal branch of depressor muscle of trochanter.  
  
*R*, radius.  
*Rd*, posterior fold, reduplication, of tergum.  
  
*S*, levator muscle of tibia sternum.  
*SA*, sternal apophysis.  
*Sa*, subalare.  
*sa*, external pit of sternal apophysis.  
*Sc*, subcosta.  
*Scl*, scutellum.  
*scl*, subdivision of scutellum.  
  
*Sct*, scutum.  
*sct*, subdivision of scutum.  
*Scx*, subcoxa.  
*Sl*, sternellum.  
*Sp*, spiracle. *Sp<sub>2</sub>*, *Sp<sub>3</sub>*, first and second thoracic spiracles.  
*Spn*, spina.  
*spn*, external pit of spina.  
*Ss*, spinasternum.  
*Stn*, primary segmental sternite.  
  
*T*, depressor muscle of tibia. tergum.  
*Tar*, tarsus.  
*Tb*, tibia.  
*tg*, tegular rudiment.  
*TmMcl*, tympanal muscle.  
*Tn*, trochantin.  
*Tr*, trochanter. *1Tr*, *2Tr*, first and second trochanters.  
*Tra*, trachea.  
  
*U*, levator muscle of tarsus.  
*Uf*, unguifer of tarsus.  
*Un*, unguis, claw.  
*Utr*, unguitractor plate.  
  
*V*, depressor muscle of tarsus.  
*VD*, vena dividens.  
*VIIISp*, eighth abdominal spiracle.  
*VMcl*, ventral longitudinal muscle.  
*VR*, ridge between scutum and scutellum.  
*vs*, scuto-scutellar suture.  
  
*W*, wing.  
*WP*, pleural wing process.  
  
*X*, depressor muscle of pretarsus, retractor of claws.

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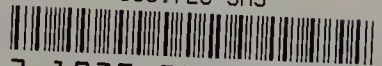








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